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EFFECTS OF FERAL PIG REMOVAL ON SOIL PROPERTIES AND BELOWGROUND CARBON CYCLING IN NATIVE HAWAIIAN MONTANE WET FORESTS

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ABSTRACT

Nonnative ungulate removal from fenced exclosures is common for restoring and conserving native ecosystems. Little is known, however, about the impacts of nonnative ungulate removal on soil properties or belowground carbon cycling. Here, I measured soil physical and chemical properties, and soil carbon pools and fluxes in paired sites inside and outside of a chronosequence of five feral pig exclosures ranging in age from 6.6 to 18.5 years in Hawaiian montane wet forests. Results demonstrate that feral pig removal improves soil structure, increases nutrient availability, and accelerates soil C cycling without changing soil C storage. Importantly, increased soil carbon cycling and nitrification were positively related to increasing time since feral pig removal. Collectively, these results demonstrate that feral pig removal improves soil physical and chemical properties and increases belowground carbon cycling, which has important implications for ecosystem restoration and conservation.

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CHAPTER 1

Introduction

Nonnative feral pigs (*Sus scrofa* Linnaeus, 1758; "wild boar" in native ranges) have invaded ecosystems on all continents, except Antarctica, and most oceanic islands (Barrios-Garcia and Ballari 2012; Wehr, Hess, and Litton, *In press*). The global introduction and spread of these animals have important consequences for terrestrial ecosystems (Spear and Chown 2009; Campbell and Long 2009; Barrios-Garcia and Ballari 2012; Hess 2016; Leopold and Hess 2017). In the United States, feral pigs are considered the greatest non-human, animal-related extinction threat to native species (Gurevitch and Padilla 2004). Feral pigs expand their range by up to 4 km^2/year (Hone 2002) due to high fecundity (up to eight piglets twice a year), high adaptability to a variety of environmental conditions (West, Cooper, and Armstrong 2009), and an omnivorous diet (Spear and Chown 2009). Feral pig foraging via rooting, grubbing and browsing, in particular, represents an important disturbance agent to soil and vegetation (Spear and Chown 2009; Barrios-Garcia and Ballari 2012; Campbell and Long 2009). Due to their rapidly expanding range and role as an important disturbance agent, increased understanding of the impacts of feral pigs on soil and vegetation is urgently needed to better inform land management.

The majority of feral pig research has focused on their impacts aboveground, particularly on vegetation, and much less attention has been directed to their potential impacts on soils (Spear and Chown 2009). In particular, there is a paucity of information on how feral pigs impact soil physical properties, soil nutrient cycling and availability, and soil carbon (C) storage and flux. Further, very few studies globally have examined the impact of feral pig removal from ecosystems to which they are nonnative, and so there is a conspicuous lack of information on ecosystem recovery rates and trajectories (Barrios-Garcia and Ballari 2012). Together, these areas represent an important knowledge gap for the restoration and conservation of native ecosystems degraded by nonnative ungulates globally.

Feral Pig Impacts on Soil Physical Properties

Maintenance of soil structure (the arrangement of primary soil particles into aggregates) and soil aggregate stability (the ability of soil aggregates to resist stress) is vital for soil productivity and environmental quality because these soil physical properties help prevent

erosion and allow for adequate gas exchange and movement of water and nutrients through soil (Amezketa 1999). Feral pigs have the potential to appreciably impact soil structure and aggregate stability as a result of their foraging and rooting activities that mix the soil profile. Feral pigs appear to disturb forest floor and soil to different degrees in different habitats: 7% of area annually in Californian coastal prairie (Kotanen 1995); 22% of area annually in mixed pine-hardwood forest in Big Thicket National Preserve (Texas, USA) (Siemann et al. 2009); and 80% of area annually in forests of Great Smokey Mountains National Park (Tennessee, USA) (Howe and Singer 1981). Furthermore, in Great Smokey Mountains National Park, feral pigs can mix soil to depths of 25 cm (Lacki and Lancia 1983) and obscure the A_1 and A_2 soil horizon boundary, reduce the O horizon by 64%, and decrease forest floor litter by as much as 59% (Singer, Swank, and Clebsch 1984). Together, these disturbances to soil have the potential to degrade soil structure by physically disrupting soil aggregates and increasing bulk density via compaction (Vtorov 1993).

Soil aggregate stability and bulk density, in turn, influence the abundance of non-burrowing soil organisms, particularly microarthropods, who are reliant upon non-compacted soil with adequate air space and stable soil structure (Vtorov 1993). Soil organisms, from microarthropods to small burrowing animals, maintain soil structure via bioturbation and fragmentation of soil organic matter (SOM) (Gabet, Reichman, and Seabloom 2003; Wilkinson, Richards, and Humphreys 2009). Disturbance by feral pigs has been implicated in decreases in: burrowing rodents in Texas (Singer, Swank, and Clebsch 1984); soil microbes and predatory soil arthropods in Germany (Mohr and Topp 2001; Mohr, Cohnstaedt, and Topp 2005); and microarthropods in Hawai‘i (Vtorov 1993). In Andisols of tropical montane wet forests on Hawai‘i Island, *Collembola* spp. (springtail, a microarthropod) density increased significantly seven years after the removal of feral pigs (Vtorov 1993). Vtorov (1993) speculated that the increase in *Collembola* spp. was associated with a threefold increase in soil porosity and improved soil structure following feral pig removal.

Soil structure and aggregate stability are partially the result of the binding of soil particles into aggregates by SOM (Amezketa 1999). The mixing of the forest floor into mineral soil by feral pigs can accelerate SOM decomposition by destabilizing soil aggregates and exposing a higher surface area of SOM to oxidative reactions and soil decomposing microbes (Craswell and Lefroy 2001), thereby increasing the active soil C pool (Brady and Weil 2010). The active C

pool facilitates soil aggregate stability and soil structure and protects macro-aggregates (particles > 250μm) (Amezketa 1999). An accelerated loss of SOM can result in a greater proportion of micro-aggregates (particles <250 μm) that are more susceptible to dispersion (Amezketa 1999). Greater dispersion, in turn, promotes soil erosion and compaction, and reduces infiltration and gas exchange (Seybold and Herrick 2001). While few, if any, studies have investigated the effects of feral pigs on soil structure and aggregate stability, prior studies have described contrasting impacts of feral pig activity on SOM pools. In Great Smokey Mountains National Park, Lacki and Lancia (1983) found an increase in SOM pools following feral pig activity. In native ranges, wild boar activity elicited no change in SOM pools in coniferous or deciduous forests in the Netherlands (Groot Bruinderink and Hazebroek 1996), or following two years of simulated bioturbation in deciduous German forests (Mohr, Cohnstaedt, and Topp 2005). However, in a different study, Mohr and Topp (2001) found that rooting by wild boars decreased SOM pools in forests of Germany. These somewhat contrasting results on SOM pools in native and introduced ranges, combined with a dearth of knowledge regarding the impacts of feral pigs on soil structure and aggregate stability, showcase the critical need for a better understanding of feral pig impacts on soil.

Feral Pig Impacts on Soil Nutrient Cycling and Availability

Soil nutrient cycling and availability are of critical importance for ecosystem structure and function, and prior studies have documented that feral pigs can directly impact soil nutrients. Soil disturbance by feral pigs reduced soil C:N as a result of mixing and incorporation of forest floor organic material into mineral soil, and accelerated nitrogen (N) mineralization in mixed pine-hardwood forest in Texas (Siemann et al. 2009). In Great Smokey Mountains National Park, nitrate (NO_3^-) concentrations were higher in soils and streams adjacent to areas disturbed by feral pigs compared to non-impacted areas (Singer, Swank, and Clebsch 1984). Feral pig activity has also been responsible for decreased cation exchange capacity (CEC) and accelerated loss of plant nutrients in both their introduced (Singer, Swank, and Clebsch 1984) and native ranges (Mohr and Topp 2001; Mohr, Cohnstaedt, and Topp 2005; Wirthner et al. 2012). In Hawai‘i, feral pigs are commonly found in forests on Andisols where non-crystalline minerals store high concentrations of SOM. In this case, soil disturbance by feral pigs may accelerate SOM

decomposition and nutrient availability, yet no prior study has quantified feral pig impacts on soil nutrient cycling in Hawai‘i.

Increased soil nutrients with feral pig activity, particularly NO_3^-, has the potential to contaminate streams and groundwater. This is particularly true in Hawai‘i where young Andisols (300 yr) have low hydraulic resistance and, thus, can leach NO_3^- more so than older substrates (Lohse and Matson 2005). Increased mineralization and availability of soil N, particularly in disturbed soils with higher water content and anaerobic conditions, can also increase the flux potent greenhouse gasses such as NO_x and N_2O to the atmosphere (Hall and Matson 2003; Pathak 1999). Foliar stable N isotope composition ($\delta^{15}N$) – an index of the ratio of the heavier (^{15}N) to the lighter (^{14}N) N isotope (Evans 2001; Robinson 2001; Kahmen, Wanek, and Buchmann 2008) – is an indicator of nitrogen cycling rates and bioavailability. Increased inorganic N availability from mineralization and nitrification (e.g., as a result of SOM decomposition) typically enriches foliar $\delta^{15}N$ (Craine et al. 2009) due to losses of ^{14}N in highly mobile gaseous and leachable forms (Evans 2001). As a result, N stable isotopes represent a potentially useful, but underutilized, method to determine the impacts of feral pigs on soil N cycling.

Given the large scale of feral pig invasion in Hawai‘i, both in duration and area (Steven C. Hess 2016; Wehr, Hess, and Litton, *In press*.), a clearer understanding of feral pig-induced changes in soil nutrients is important, particularly in the context of vegetation communities. Soil disturbance by nonnative feral pigs in Hawai‘i has been linked to the establishment and spread of a number of nonnative plants, including *Erharta stipoides* (Aplet, Anderson, and Stone 1991), *Myrica faya* (Aplet, Anderson, and Stone 1991; Vitousek and Walker 1989) and *Psidium cattleianum* (Diong 1982; Huenneke and Vitousek 1990; Nogueira-Filho, Nogueira, and Fragoso 2009). The success of nonnative plants in the presence of feral pig disturbance is thought to be the result of a combination of an initial disturbance that creates a window of opportunity for invasion, greater soil nutrient and light availability following feral pig disturbance, and high resource-use efficiency in nonnative plants (Knauf et al., *In review*). That is, nonnative plants are better adapted to increased soil nutrients and grow quicker than native plants following feral pig activity. This is an important, but untested, mechanism that has large implications for conservation and restoration of native Hawaiian forest ecosystems that are impacted by feral pigs.

Feral Pig Impacts on Soil Carbon Storage and Flux

There is increasing focus on determining the impact of invasive species on ecosystem C sequestration (Peltzer et al. 2010). For instance, changes in plant community composition associated with the introduction of nonnative grazers can reduce soil C by 49% (Bagchi and Ritchie 2010). Despite the near ubiquitous spread of feral pigs throughout the world and their ability to disturb soil and vegetation (Barrios-Garcia and Ballari 2012), there has been very little research into the potential impacts of feral pigs on ecosystem C cycling, particularly belowground. Any impacts of feral pigs on soil C are important given the magnitude of soil C storage globally in terms of both size and longevity (Brady and Weil 2010). Globally, soils contain 2,273 Pg C in the top 2 m of the soil profile (Jackson et al. 2017), which is more than twice the amount of C contained in vegetation and the atmosphere combined (Jackson et al. 2017). Forest ecosystems, in particular, contain large pools of soil C, and tropical forests contain more soil C than temperate and boreal forests combined (Jobbagy and Jackson 2000). The majority of forest soil C is typically located within the upper 20 cm of the soil profile (Jobbagy and Jackson 2000), making it particularly vulnerable to feral pigs which root, grub and dig to depths up to 25 cm (Lacki and Lancia 1983). Feral pig disturbance can alter SOM decomposition and reduce vegetation cover, which together or alone have the potential to alter the flux of C into and out of soil and, therefore, soil C storage.

The primary C inputs to soil are aboveground litterfall (F_L) and total belowground C flux (TBCF; the allocation of C to belowground by plants as root exudates, and to support the growth and maintenance of roots and mycorrhizae) (Raich and Nadelhoffer 1989; Giardina and Ryan 2002). Under steady state conditions, with no change in mineral soil C (C_{Soil}), litter layer C (C_{Litter}), or root biomass C (C_{Root}) pools over time, TBCF can be estimated via mass balance as the difference between soil-surface CO_2 efflux (*Fs*; the combination of belowground and heterotrophic respiration (Ryan and Law 2005)) and F_L (Raich and Nadelhoffer 1989). In non-steady state conditions where there are appreciable or unknown changes in soil C over time (e.g., rapidly aggrading forests recovering from disturbances), TBCF is estimated as the difference between F_S and F_L plus any change in C_{Soil}, C_{Litter}, and C_{Root} over time (Nadelhoffer, Raich, and Aber 1998; Giardina and Ryan 2002; Litton, Ryan, and Knight 2004).

Prior research has shown mixed impacts to soil C pools by feral pigs. For example, feral pig activity increased C_{Soil} in Tennessee high elevation beech gaps (Lacki and Lancia 1983), yet

had no effect on C_{Soil} under oak canopies or grasslands on Santa Cruz Island, California (Moody and Jones 2000). Elsewhere, C_{Litter} was reduced by feral pigs due to mixing of the litter layer into the soil profile in Texan mixed pine-hardwood forest (Siemann et al. 2009), Tennessee deciduous forests (Singer, Swank, and Clebsch 1984) and Australian lowland tropical rainforests (Taylor, Leung, and Gordon 2011). Conversely, no changes in soil C pools were seen in Australian highland tropical rainforests (Mitchell et al. 2007). C_{Root} can be affected directly by feral pig depredation (Schley and Roper 2003; Taylor and Hellgren 1997; Chimera et al. 1995; Pavlov and Edwards 1995), or indirectly via changes in C allocation as a result of alterations in soil nutrient availability (Litton, Raich, and Ryan 2007). These prior studies suggest that feral pigs likely impact soil C storage, but no study to my knowledge has investigated feral pig impacts on soil C storage in with the context of impacts on soil C flux, which is crucial for understanding overall soil C dynamics (Kuzyakov 2011). It is the balance of C inputs and outputs to soils that determines the magnitude of soil C storage.

Feral pig disturbance provides a possible mechanism for altering soil C flux via physical alteration of the soil profile and increased nutrient availability. F_S is positively correlated with fine root biomass (Y. Li et al. 2004; Vargas and Allen 2008; Kuzyakov 2006; Metcalfe et al. 2007; Silver et al. 2005). Root biomass, in turn, could potentially be negatively impacted by physical alterations to soil and depredation by feral pigs. Any change in F_S associated with feral pig activity is important to understand, as F_S is the second largest flux in the terrestrial C cycle behind only gross primary productivity (Raich & Schlesinger 1992). As a result, small increases in F_S have the potential to substantially increase atmospheric CO_2 levels (Bond-Lamberty and Thomson 2010). In turn, TBCF typically decreases with increasing nutrient supply, with a concomitant increase in C flux to aboveground (Litton, Raich, and Ryan 2007). Increased C flux to aboveground, in turn, can increase soil C input via litterfall. Together, potential changes in the flux of C into (TBCF and F_L) and out of (F_S) soil can alter soil C pools in feral pig invaded ecosystems, yet no prior study has quantified the impacts of feral pigs on overall belowground C cycling.

To my knowledge, only one prior study has investigated the impacts of *S. scrofa* on F_S, and this study occurred in their native range. Risch et al. (2010) found that in Switzerland, three years of wild boar grubbing increased F_S by 23%. The authors attributed the increase in F_S to the incorporation of litter C into mineral soil which enhanced SOM decomposition, increased gas

diffusion rates, and resulted in higher fine root and microbial biomass. While wild boar activity was shown to increase F_S in Swiss forests in this prior study, the study did not investigate fluxes of C to belowground that could potentially offset increased F_S resulting from wild boar activity (i.e., F_L and TBCF). Other studies have shown that increased F_S in the context of rising temperatures did not alter soil C storage because of a concomitant increase in the flux of C to belowground via F_L and TBCF (Giardina et al. 2014).

Feral Pig Management in Hawai‘i

Feral pig introduction to the Hawaiian Islands first occurred between 1000 and 1200 AD with the arrival of ancient Polynesians who brought with them a smaller Polynesian variety of *Sus scrofa* (Wehr, Hess, and Litton, *In press*). Subsequent arrivals to Hawai‘i by Captain James Cook in 1778-1779, and later European settlers, introduced the larger European wild boar and domesticated lineages of swine, which interbred with the Polynesian variety to produce the feral pigs found throughout the Hawaiian Islands today, as well as on many other Pacific Islands (Linderholm et al. 2016; Wehr, Hess, and Litton, *In press*). Since their introductions, feral pigs have proliferated and degraded native Hawaiian ecosystems (Hess 2016; Cole and Litton 2014; Wehr, Hess, and Litton, *In press*), and prompted the construction of fenced management units (i.e., ungulate exclosures) around areas of high conservation value throughout Hawai‘i and the Pacific Island Region (Hess 2016; Hess and Jacobi 2011).

Nonnative ungulate exclosures are expensive to construct and maintain, particularly for feral pigs. Incidentally, ungulate removal is time- and cost-intensive, so exclosures are typically completed incrementally across an invaded ecosystem with new exclosures constructed adjacent, or in close proximity, to existing exclosures. Thus, an invaded ecosystem will be protected by exclosures of different ages since feral pig removal (i.e. chronosequenced of removal), which represents a valuable model study system to investigate ecosystem responses to increasing time since feral pig removal.

Recent studies on Hawai‘i Island have shown significant positive responses of understory plants to the removal of feral pigs from large exclosures (Cole et al. 2012; Cole and Litton 2014). For instance, establishment of woody vegetation (both native and nonnative) on the forest floor and forest floor litter cover increased along an 18.5 year chronosequence of feral pig exclosures (Cole and Litton 2014), and stand density of young native tree ferns increased significantly 16 years after feral pig removal from native Hawaiian tropical montane wet forests (Cole et al.

2012). Reducing feral pig impacts to tree fern abundance and mortality can promote establishment sites for native vegetation (Murphy et al. 2014). Furthermore, Drake & Pratt (2001) found that native seedling mortality decreased with the removal of feral pigs.

Scope of Research

The research summarized in my thesis utilizes a chronosequence of five feral pig exclosures, ranging in age from 6.6 to 18.5 years, to determine the impacts of feral pig removal on soil physical and chemical properties (Chapter 2) and soil C cycling (Chapter 3) in native Hawaiian tropical montane wet forests. The study area is representative of some of the last remaining intact native forests in Hawai‘i where 87% of the species are native, of which 83% are endemic (Cole and Litton 2014). Additionally, soil C in these forests exceeds 30 kg m^{-2} (Schuur, Chadwick, and Matson 2001), which is in excess of the global average for tropical evergreen forests (Jobbagy and Jackson 2000), highlighting the importance of soil C in these forests and the need for research into possible impacts by feral pigs.

Prior research on feral pig impacts to ecosystem function and services has commonly focused on recent invasions (Barrios-Garcia and Ballari 2012). In contrast, this research investigates the impacts of feral pig removal from native Hawaiian tropical montane wet forests, and provides information on ecosystem recovery trajectories and rates. Results from this research will inform both basic and applied science by filling an important gap in scientific understanding of the impacts of feral pig removal on soil biogeochemistry, and by providing land managers with information to guide management of forests invaded by feral pigs.

CHAPTER 2

Impact of nonnative feral pig removal on soil structure and nutrient availability in Hawaiian tropical montane wet forests

Abstract

Conservation and restoration of degraded ecosystems often includes the removal of nonnative ungulates and is assessed by tracking vegetation response. However, the impacts of nonnative ungulate removal on underlying ecosystem processes, e.g., soil structure and nutrient availability, is usually poorly characterized despite their large role in driving vegetation dynamics. To address this, I quantified how removal of nonnative feral pigs (*Sus scrofa*) from Hawaiian tropical montane wet forests affects soil physical and chemical properties that characterize soil structure and nutrient availability. Primary measurements were made in randomly located paired sites inside and outside of five feral pig removal units representing a 6.6 to 18.5 year chronosequence. Additional sites were sampled inside and outside of the second oldest exclosure in locations visibly characterized as low and high impact areas. Results from the chronosequence and targeted plots were similar in direction, with the largest differences generally observed in the targeted plots. Nonnative feral pig removal from these sites improved soil structure as evidenced by an increase in stable soil aggregates and porosity, and a decrease in bulk density, water-filled pore space, and soil moisture content. Further, feral pig removal generally increased the cycling and availability of soil nutrients, with increased extractable cations and N mineralization, and enriched foliar $\delta^{15}N$. Additionally, increasing time since feral pig removal was positively related to nitrification and negatively related with ammonification. Changes in soil structure and nutrient availability with feral pig removal coincided with, and likely contributed to, large increases in understory vegetation density and abundance.

Introduction

Nonnative species invasions impact ecosystem function and services (R. N. Mack et al. 2000; Vitousek et al. 1996; M. C. Mack and D'Antonio 1998; Ehrenfeld 2003), and burden local and national economies (Pejchar and Mooney 2009; Pimentel et al. 2000). Nonnative ungulates can be particularly destructive, often resulting in the extirpation of native taxa and facilitation of nonnative plant invasions (Spear and Chown 2009; Nuñez, Bailey, and Schweitzer 2010; Oduor, Gómez, and Strauss 2010; Campbell and Long 2009). Nonnative ungulates can also transmit soil-borne pathogens, parasites and zoonotic diseases (Krull, Waipara, et al. 2013; Barrios-Garcia and Ballari 2012; A. Y. Li et al. 2013). As a result, nonnative ungulate control is often a high priority for the conservation and restoration of native ecosystems (Spear and Chown 2009; Courchamp, Chapuis, and Pascal 2003).

Nonnative ungulate removal from fenced management units (i.e., ungulate exclosures) is an increasingly common management strategy globally. Within exclosures, both native and nonnative vegetation have been shown positive responses (Weller et al. 2011; Stone, Cuddihy, and Tunison 1992; Tanentzap et al. 2009; Cole and Litton 2014), suggesting that management following ungulate removal should include active vegetation management (Stone, Cuddihy, and Tunison 1992; Cole et al. 2012; Nuttle, Ristau, and Royo 2014; Cole and Litton 2014). Alterations to soils by nonnative ungulates may explain why vegetation recovery following ungulate removal can vary, or even be dominated by nonnative plants however, this topic has received little attention (Spear and Chown 2009; Kardol et al. 2014; Cole and Litton 2014; Campbell and Long 2009). In particular, little is known about the extent or rate at which soil structural properties or nutrient availability recovers following the removal of nonnative ungulates.

Ungulates can increase soil organic matter (SOM) mineralization and alter the availability of nutrients (Siemann et al. 2009; Hobbs 1996; Frank et al. 2000; Palacio et al. 2013) thereby impacting plant community composition (Stohlgren, Schell, and Heuvel 1999). Nonnative plants can take advantage of resource pulses and outcompete native species (Funk and Vitousek 2007; Ostertag and Verville 2002). Furthermore, ungulates can compact soils (Vtorov 1993) and reduce soil aggregate stability (Beever, Huso, and Pyke 2006), causing a breakdown in soil structure that at least partially controls the availability and uptake of plant nutrients (Brady and Weil 2010). A better understanding of how ungulate removal impacts soil structure

and nutrient availability should provide critical information to land managers tasked with conserving and restoring native ecosystems impacted by nonnative plant and ungulate invasions.

Nonnative feral pigs (*Sus scrofa* Linnaeus, 1758; "wild boar" in native ranges) are a particularly destructive ungulate, with often large impacts on oceanic islands and all continents except Antarctica (Barrios-Garcia and Ballari 2012). However, most existing research has focused on how these animals alter the structure and diversity of plant communities, with less attention on the impacts on soil properties (Spear and Chown 2009; Barrios-Garcia and Ballari 2012). Findings from the few studies that have examined wild boar impacts on soils in both their native and introduced ranges have been inconsistent. For example, wild boar soil disturbance decreased bulk density in Tennessee deciduous forests (Singer, Swank, and Clebsch 1984), while in a native Hawaiian montane wet forest, bulk density decreased within seven years of their removal (Vtorov 1993). In both cases, soil disturbances decreased soil fauna diversity and abundance (Singer, Swank, and Clebsch 1984; Vtorov 1993). Wild boar impacts on SOM and nutrient availability have been variable. For example SOM decomposition, cation exchange capacity and acidity increased with disturbance in high elevation beech gaps (Lacki and Lancia 1983), while wild boar removal had no effect on N mineralization and pH under oak canopies and grasslands on Santa Cruz Island, California (Moody and Jones 2000). In Texan mixed pine-hardwood forest, wild boar lowered soil carbon (C):nitrogen (N), presumably due to accelerated N mineralization (Siemann et al. 2009). Wild boar disturbance also increased N mineralization in deciduous forest (Singer, Swank, and Clebsch 1984), yet had no significant impact on N mineralization in a coastal California grassland (Cushman, Tierney, and Hinds 2004).

Alterations to soil properties by wild boar in their home ranges are similarly inconsistent in the literature. In Spanish alpine grasslands, wild boar disturbances decreased soil moisture, C:N, ammonium (NH_4^+) and extractable Na, Mg, and Ca in soil solution, while increasing bulk density, total N, and nitrate (NO_3^-) (Bueno et al. 2013). Wild boar rooting did not affect SOM in the Netherlands (Bruinderink and Hazebroek 1996), yet increased SOM and decreased inorganic N availability in Switzerland (Wirthner et al. 2012). Inconsistent effects of wild boar in these and other studies may also be an artifact of the sampling scheme, statistical methods employed and heterogeneity of ecological systems, where low sample sizes and/or inherent variability can obscure real treatment effects of nonnative ungulates (Davidson and Hewitt 2014).

In Hawai‘i, in the late 18th century, European explorers and settlers introduced European wild boar, which subsequently interbred with a smaller Polynesian variety that had been introduced and domesticated by Polynesian settlers centuries prior (Wehr, Hess, and Litton, *In press*). Here, I use the term “feral pig” to refer to the mixed Polynesian and European pigs that have proliferated throughout Hawai‘i (Hess 2016; Leopold and Hess 2017; Wehr, Hess, and Litton, *In press*).

Ungulate exclosures have been widely used to protect and restore invaded Hawaiian ecosystems (Scowcroft and Hobdy 1987; Stone, Cuddihy, and Tunison 1992; Cole and Litton 2014; Hess and Jacobi 2011). This current study utilized a chronosequence of feral pig exclosures and experimental design established by Cole and Litton (2014), who found that native understory stem density, species richness and ground-rooted woody plants, were much greater within feral pig–free exclosures than adjacent pig present areas. Coupled with vegetation recovery, these authors documented an increase in forest floor litter and bryophyte cover, and a decrease in exposed soil (Cole and Litton 2014). Unknown, however, is if there were changes in underlying soil properties that may have facilitated vegetation recovery. Here, I examined the impacts of feral pig removal, and time since removal on soil structure and nutrient availability by measuring a suite of soil physical and chemical properties across the chronosequence. Additionally, I compared the same suite of soil properties inside and outside of a single exclosure in plots targeted for recent heavy feral pig disturbance (i.e., digs and wallows) vs. areas with historically low disturbance (i.e., areas naturally protected from feral pig disturbance between fallen trees or other natural barriers) to control for heterogeneity of soil properties and feral pig disturbance.

I hypothesized that soil structure would improve (e.g., decreased bulk density, increased soil aggregation) and soil nutrient availability would increase as a result of feral pig removal, understory vegetation recovery, and increased forest floor (Cole and Litton 2014). I also hypothesized that, as vegetation recovers within the exclosures, soil structure and nutrient availability would increase with increasing time since feral pig removal. Additionally, I expected the direction of changes to be the same between chronosequence and targeted plots, and the magnitude of change will be higher in targeted plots.

Methods

Study Sites

This study was conducted between August 2010 and December 2012 along a chronosequence of five feral pig exclosures ranging 6.6 - 18.5 years since feral pig removal, and in targeted plots inside and outside of the 16.5 year-old exclosure, on the East flank of Mauna Loa Volcano on the Island of Hawai‘i (Figure 2.1; Cole and Litton 2014). Estimated feral pig densities in surrounding forest range 0.6 - 16.3 animals/km^2 (Scheffler et al. 2012). Study sites are located between 1,140 and 1,370 m.a.s.l. Mean annual temperature and precipitation range 14.4 - 15.9 °C and 2,910 - 3,985 mm, respectively, with little seasonality (Giambelluca et al. 2013, 2014). Study sites are located on 2,000 – 10,000 year-old, tephra-derived Andisols of two closely related series: Eheuiki (medial, ferrihydritic, isothermic Typic Hydrudands) and Puaulu (medial over ashy, aniso, ferrihydritic over amorphic, isothermic Aquic Hapludands) (NRCS 2010). These soil series are characterized by deep, moderately well drained soils formed in basic volcanic ash deposited over basic lava with slopes of 2-5% (NRCS 2010). All study sites are located in *Metrosideros polymorpha* Gaudich. (overstory tree)/*Cibotium* spp. (midstory tree fern) tropical montane wet forest (Wagner, Herbst, and Sohmer 1990) with exclusively native canopy vegetation (Cole and Litton 2014).

Along the chronosequence, pairs of sites were established inside and outside of each exclosure, where each site consisted of four circular 18 m radius (1,018 m^2) sampling plots located > 70 m from fence lines and > 140 m from each other. Targeted sites were located inside and outside of the 16.5 year-old feral pig exclosure, where ten 6 m^2 plots were established along a 150 m transect outside the exclosure in areas targeted for recent heavy feral pig disturbance (e.g., digs and wallows), and ten 6 m^2 plots were established along a separate 150 m transect inside the exclosure in areas targeted for historically low disturbance (i.e., areas naturally protected from feral pig disturbance between fallen trees or other natural barriers). Although the targeted plots were located inside and outside a single exclosure and, therefore, pseudo-replicated, they were designed to: control for the inherent spatial heterogeneity of soil properties and feral pig disturbances; estimate maximal differences in soil properties following the removal of feral pigs; and corroborate chronosequence results.

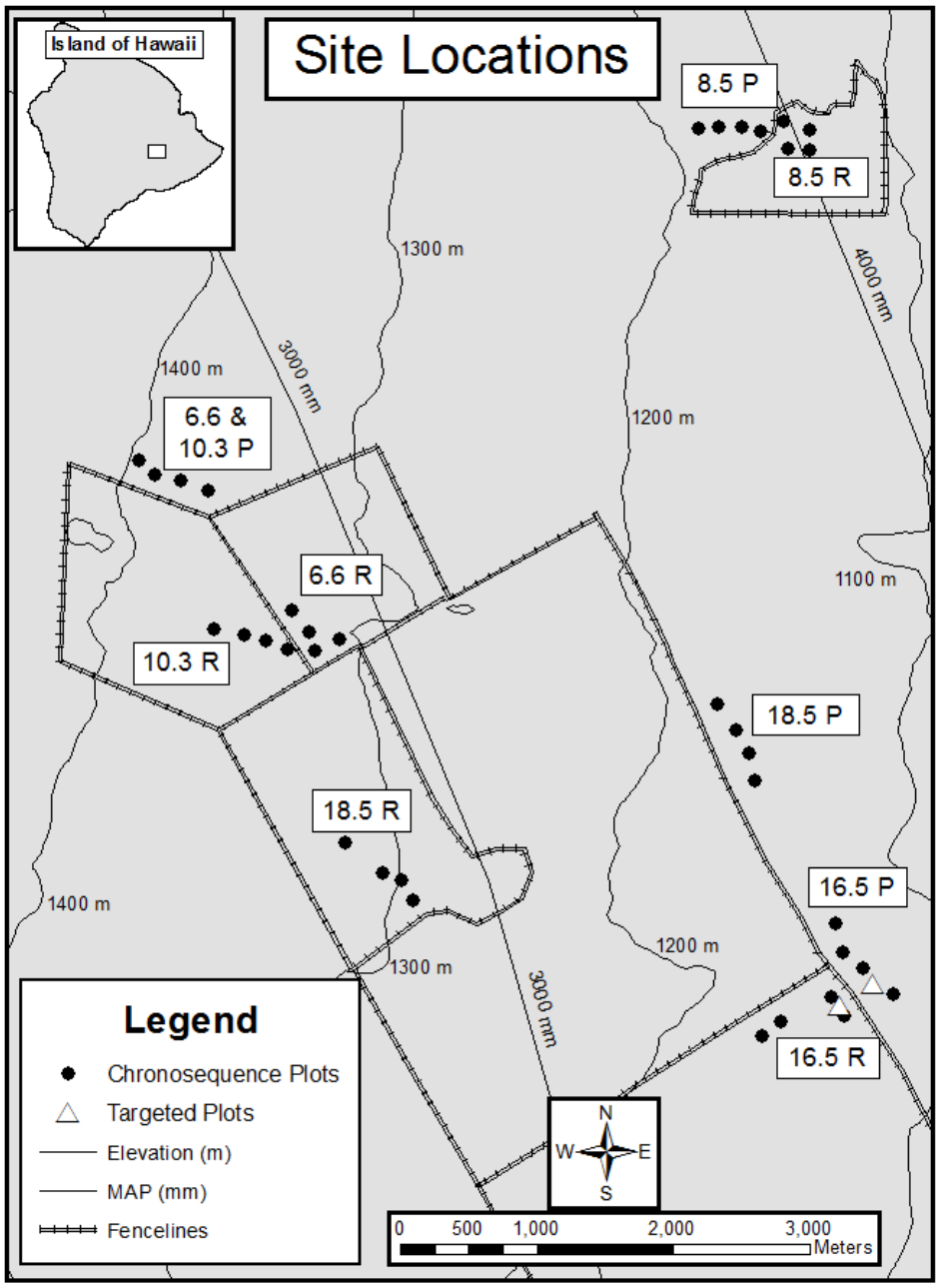

Figure 2.1 Study site locations inside and outside of feral pig exclosures on the East slope of Mauna Loa Volcano, Island of Hawai‘i. Paired study sites are labeled by years since feral pig removal and feral pig presence (P) or feral pig removal (R)

Soil Sampling

For all chronosequence and targeted plots, I measured volumetric water content (VWC), bulk density, porosity, water-filled pore space, water-stable soil macro-aggregates (>250 μm; WSA), resin available inorganic N (NO_3^- and NH_4^+), net N mineralization (NO_3^- and NH_4^+), pH, extractable nutrients (P, K, Ca, and Mg), mineral soil organic carbon (SOC) and soil organic nitrogen (SON), and hot water soluble C (i.e., labile SOC) in the top 10 cm of soil. I also measured foliar $\delta^{15}N$ of the three dominant species in the overstory and midstory in the chronosequence plots as an index of soil nutrient cycling and availability (Craine et al. 2009).

Over four consecutive days of comparable weather, ten uniformly arrayed soil cores were collected within each chronosequence plot and three soil cores were taken from random locations within each targeted plot using a 10 cm tall x 5.1 cm diameter soil corer. Soil cores were composited by plot, immediately transported in coolers to a refrigerator, and processed within 48 hours of collection. Roots and rocks > 0.6 cm in each composited sample were removed by hand and sieve, and soils were weighed and homogenized for analyses.

The allophone and imogolite dominated Andisols of my study system are characterized by aluminum-humus complexes that promote strong stable aggregates (Nanzyo 2002; Perret and Dorel 2006). As these soils dry, their colloidal fraction irreversibly solidifies into pseudo-sands that cannot be rewetted (Nanzyo 2002; Perret and Dorel 2006). Consequently, all analyses except SOC, SON and bulk density were determined on fresh soil samples.

Soil Analyses

To determine SOC and SON, homogenized sub-samples of field-moist soil were oven-dried at 70 °C to a constant mass and passed through a 2 mm (#10) sieve. A representative sub-sample was ball-milled, passed through a 0.5 mm (#40) sieve, and analyzed for SOC and SON with a Costech Elemental Analyzer (Costech Analytical Technologies Inc., Valencia, CA) at the University of Hawai‘i at Hilo Analytical Laboratory. Bulk density (g cm^{-3}) was determined after oven-drying two weighed sub-samples of field-moist soil at 105 °C to a constant mass (~ 24 h), averaging their percent water losses and estimating the 105 °C dry weight equivalent of the bulk soil collection. Bulk density (g cm^{-3}) was calculated as:

$$BD = (DW_{sample105}) / V_{core} \quad \text{[Eq. 1]}$$

Where $DW_{sample105}$ is the estimated dry weight of the bulk sample and V_{core} is the total volume of the bulk sample.

Soil VWC was measured with a Hydrosense CS620 Water Content Sensor (Campbell Scientific, Logan, UT) at twelve locations distributed systematically within the chronosequence plots, and at eight random locations within the targeted plots. Soil porosity (%) was calculated using a particle density of 2.65 g cm^{-3} (Soil Survey Staff 2014) and was used to calculate water-filled pore space (%) (Soil Survey Staff 2014).

Water stable macro-aggregates (WSA) >250 µm are the aggregate size class most vulnerable to physical disturbance (Seybold and Herrick 2001), and I quantified WSA in this size class using the wet-sieving procedure from the USDA NRCS Soil Quality Test Kit (2001). Pseudo-sands formed by aluminum-humus complexes in Andisols resist standard dispersion methods (Silva et al. 2014) and preclude quantifying sand content in WSA. A ~14 g sub-sample of homogenized field-moist soil was placed onto a 250 µm sieve that was moved vertically 1.5 cm in DI water at 30 cycles per min for 3 min. Material >250 µm was oven-dried at 105°C for 24 h and weighed. A second ~12 g sub-sample was weighed, dried at 105°C for 24 h and reweighed to determine gravimetric water content and calculate the dry weight of the field-moist sieved sample. WSA was calculated as:

$$\% \text{ WSA} = M_{WS}/M_{dry} * 100 \quad \text{[Eq. 2]}$$

Where M_{WS} is the dry mass of WSA (g) and M_{dry} is the dry weight of the sample prior to sieving.

Resin available inorganic nitrogen (NO_3^- and NH_4^+; µg N 10 cm^{-2} 4 $weeks^{-1}$) was estimated with a 4-week deployment of Plant Root Simulator (PRS) Probes (Western Ag Innovations, Saskatchewan, Canada). In each chronosequence plot, eight pairs of probes (one NO_3^- and one NH_4^+ probe per pair) were uniformly distributed within a 9 m radius plot centered on the larger 18 m radius plot. In each targeted plot, four pairs of probes were inserted at random locations. Foliar $\delta^{15}N$ was quantified as an index of the cycling and availability of soil N in chronosequence plots using one recently expanded sunlit leaf from three individuals each of *Cibotium glaucum* (Sm.) Hook. & Arn. (tree fern), *Cheirodendron trigynum* (Gaudich.) A. Heller (mid-canopy tree) and *M. polymorpha* (canopy tree) in each plot. These three species comprise > 95% of stand basal area across all study sites (Cole and Litton 2014). Foliage samples were

oven-dried at 70°C, ball-milled to pass through a #60 sieve, and analyzed for $\delta^{15}N$ on an isotope ratio mass spectrometer (Model DeltaV, Thermo) at the Cornell University Stable Isotope Laboratory, Ithaca, NY.

Net N mineralization (N_{MIN}) was determined with a 2M KCl extraction following a 30 d laboratory aerobic incubation with soil moisture held at field capacity. Extracts were analyzed for NH_4^+ and NO_3^- concentrations using an AutoAnalyzer (Pulse Instrumentation, Labtronics) at the University of Hawai'i at Hilo Analytical Laboratory, Hilo, HI. The labile C pool was estimated via hot-water extraction described in Ghani et al. (2003) with the omission of the initial extraction of 20°C water soluble C. Extracted labile C (μg C mL^{-1}) was quantified on a Shimadzu TOC-V Total Organic Carbon Analyzer (Shimadzu Scientific Instruments, Columbia, MD) at the University of Hawai'i at Hilo Analytical Laboratory, Hilo, HI.

Soil pH, and extractable P, K, Ca, and Mg were determined at the University of Hawai'i at Mānoa Agricultural Diagnostics Service Center, Honolulu, HI. Extractable P was quantified with the Modified-Truog method and colorimetric analysis with an autoanalyzer, while K, Ca and Mg were determined via ammonium acetate extraction and atomic absorption spectrophotometer. These extractable nutrients are reported as volumetric concentrations to include observed differences in soil bulk density with feral pigs and following their removal.

Statistical Analyses

To determine if feral pig removal had a significant effect across the chronosequence sites, one-sided Wilcoxon signed-rank tests were conducted on differences between site mean values in each pair of sites ($n = 5$), where site mean values were an average of the four replicate plots for each soil property. The effect of time since feral pig removal on each soil property across the chronosequence sites ($n = 5$) was assessed with linear regression analyses of time since removal versus the percent relative difference in site means of each soil property between paired sites:

$$[(\text{Feral pig removal} - \text{Feral pig present}) / \text{Feral pig present}] * 100 \qquad \text{[Eq. 3]}$$

The effect of feral pig removal between the targeted sites was analyzed using one-sided non-parametric Mann-Whitney U tests ($n = 10$). Results from the targeted plots were determined to be non-normal via Anderson-Darling tests on bootstrapped treatment means (2000 iterations; $P < 0.05$) with satisfactory homogeneity of variance (non-parametric Levene's test; $P > 0.10$). All statistical analyses were conducted using Minitab 16 statistical software (State College, PA)

with $\alpha = 0.10$ for significant differences. Treatment means ± 1 standard error (S.E.) are reported throughout for both chronosequence and targeted plot results.

Results

In the chronosequence plots, feral pig removal decreased bulk density (0.32 ± 0.06 and 0.23 ± 0.03 g cm^{-3} for feral pig present and feral pig removal, respectively; W = 14, $P = 0.05$, $n = 5$; Fig. 2.2a), VWC (66.6 ± 2.2 and 58.6 ± 5.0 %, respectively; W = 14, $P = 0.05$, $n = 5$; Fig. 2.2b), and water-filled pore space (76.4 ± 1.3 and 71.5 ± 3.0 %, respectively; W = 14, $P = 0.05$, $n = 5$; Fig. 2.2c), while increasing soil porosity (88.0 ± 2.3 and 91.3 ± 0.9, respectively; W = 14, $P = 0.05$, $n = 5$; Fig. 2.2d). Feral pig removal increased extractable K (135.8 ± 27.1 and 206.6 ± 28.6 µg cm^{-3} for feral pig present and feral pig removal, respectively), Ca (1729.1 ± 92.7 and 2063.1 ± 124.2 µg cm^{-3}, respectively) and Mg (350.4 ± 13.8 and 435.5 ± 19.7 µg cm^{-3}, respectively) (W = 15, $P = 0.03$, $n = 5$; Fig. 2.3a-c). Feral pig removal enriched *C. trigynum* foliar $\delta^{15}N$ (-7.3 ± 0.7 and -6.6 ± 0.9 ‰ for feral pig present and feral pig removal, respectively; W = 13, $P = 0.09$, $n = 5$) and had no impact on *M. polymorpha* (W = 8, $P = 0.50$, n = 5) or *C. glaucum* foliar $\delta^{15}N$ (W = 12, $P = 0.14$, $n = 5$) (Fig. 2.4). Feral pig removal had no impact on: WSA (W = 6, $P = 0.39$, $n = 5$; Fig. 2.2e); SOC (W = 10, $P = 0.79$, $n = 5$), SON (W =12, $P = 0.91$, $n = 5$), and labile C (W = 3, $P = 0.14$, $n = 5$) (Fig. 2.5a-c); % N (W = 3, $P = 0.14$, $n = 5$), % C (W = 3, $P = 0.14$, $n = 5$), and C:N (W = 7, $P = 0.50$, $n = 5$) (Fig. 2.6a-c); extractable P (W = 13, $P = 0.94$, $n = 5$) and pH (W = 8, $P = 0.61$, n = 5) (Fig. 2.3d-e); resin available NH_4^+ (W = 4, $P = 0.21$, $n = 5$), NO_3^- (W = 6, $P = 0.4$, $n = 5$), and total inorganic N (W = 5, $P = 0.30$, $n = 5$) (Fig. 2.7a-c); and $N_{(MIN)}$ (W = 5, $P = 0.30$, $n = 5$).

Increasing time since feral pig removal was negatively and linearly related to soil pH ($F_{(1,3)} = 16.74$, $R^2 = 0.85$, $P = 0.03$, $n = 5$) and net ammonification ($F_{(1,3)} = 95.34$, $R^2 = 0.97$; $P < 0.01$, $n = 5$; Fig. 2.8a). In addition, increasing time since feral pig removal was positively and linearly related to net nitrification and $N_{(MIN)}$ ($F_{(1,3)} = 6.21$, $R^2 = 0.67$, $P = 0.08$, $n = 5$ and $F_{(1,3)} = 5.73$, $R^2 = 0.66$, $P = 0.10$, $n = 5$ respectively; Fig. 2.8b-c). Increasing time since feral pig removal had no effect on any other soil property in the chronosequence plots ($R^2 < 0.60$; $P > 0.12$, $n = 5$).

In the targeted plots, feral pig removal reduced: VWC (79.0 ± 4.0 and 62.6 ± 2.5 % for feral pig present and removal targeted plots, respectively; W = 138.5, $P < 0.01$, $n = 10$; Fig. 2.2b) and water-filled pore space (79.0 ± 4.0 and 62.6 ± 2.5 %, respectively; W = 143.0, $P < 0.01$, $n = 10$; Fig. 2.2c); SOC (4325.4 ± 379 and 3793.2 ± 141.1 g m^{-2}, respectively; W = 105.0,

P = 0.07, *n* = 10; Fig 2.5a) and SON (298.7 ± 27.7 and 247.5 ± 13.3 g m^{-2}, respectively; W = 128.0, *P* = 0.04, *n* = 10; Fig. 2.5b);and extractable P (37.0 ± 9.3 and 16.5 ± 1.7 µg cm^{-3}, respectively; W = 132.0, *P* = 0.05, *n* = 10; Fig. 2.3d) and soil pH (5.6 ± 0.1 and 5.4 ± 0.1, respectively; W = 136.5, *P* < 0.01, *n* = 10; Fig. 2.3e). Feral pig removal increased: WSA (52.3 ± 4.5 and 70.0 ± 3.2 %, respectively; W = 69.0, *P* < 0.01, *n* = 10; Fig. 2.2e); labile C (2520.9 ± 377.5 and 3409.5 ± 390.6 µg C g^{-1}, respectively; W = 81.5, *P* = 0.04, *n* = 10; Fig. 2.5c); and C:N (14.6 ± 0.4 and 15.5 ± 0.3, respectively; W = 82.0, *P* = 0.04, *n* = 10; Fig. 2.6c). Feral pig removal reduced resin available NH_4^+ (5.0 ± 1.2 and 0.9 ± 0.2 µg 10cm^{-2} 4wk^{-1}, for feral pig present and removal targeted plots, respectively; W = 88.0, *P* < 0.01, *n* = 10) and increased resin available NO_3^- (9.3 ± 3.1 and 100.1 ± 43.4 µg 10cm^{-2} 4wk^{-1}, respectively; W = 380, *P* < 0.01, *n* = 10) and total inorganic N (14.3 ± 2.8 and 101.1 ± 43.4 µg 10cm^{-2} 4wk^{-1}, respectively; W = 43.0, *P* = 0.03, *n* = 10) (Fig. 2.6a-c). Feral pig removal had no impact on: bulk density (W = 122.0, *P* = 0.11, *n* = 10) and porosity (W = 88.0, P = 0.11, *n* = 10) (Fig. 2a,d); extractable K (W = 103.0, *P* = 0.91, *n* = 10), Ca (W = 107.0, *P* = 0.91, *n* = 10), and Mg (W = 108.0, *P* = 0.85, *n* = 10) (Fig. 3a-c); % N (W = 105.0, *P* = 0.50, *n* = 10) and % C (W = 100.0, *P* = 0.73, *n* = 10) (Fig. 2.6a-b); and $N_{(MIN)}$ (W = 98.0, *P* = 0.31, *n* = 10).

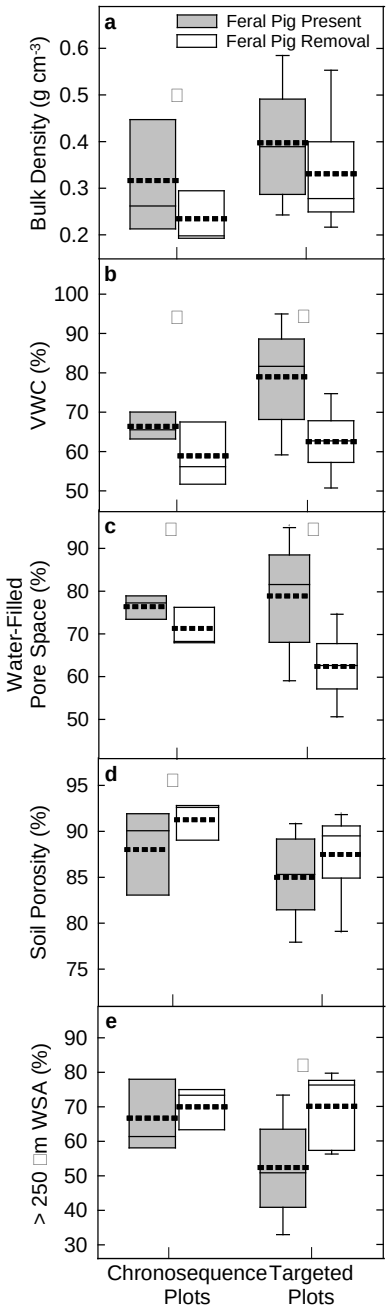

Figure 2.2 Decreases in (a) bulk density in the chronosequence plots, and (b) volumetric water content, and (c) water-filled pore space in both the chronosequence and targeted plots following feral pig removal. Increases in (d) soil porosity in the chronosequence plots and (e) percent water stable soil macro-aggregates (WSA) in the targeted plots. Whiskers indicate 10% and 90% values for the targeted plots (no whiskers are presented for chronosequence plots due to small sample size); dotted lines indicate mean and solid lines indicate median values; asterisks indicate significant differences ($\alpha = 0.10$)

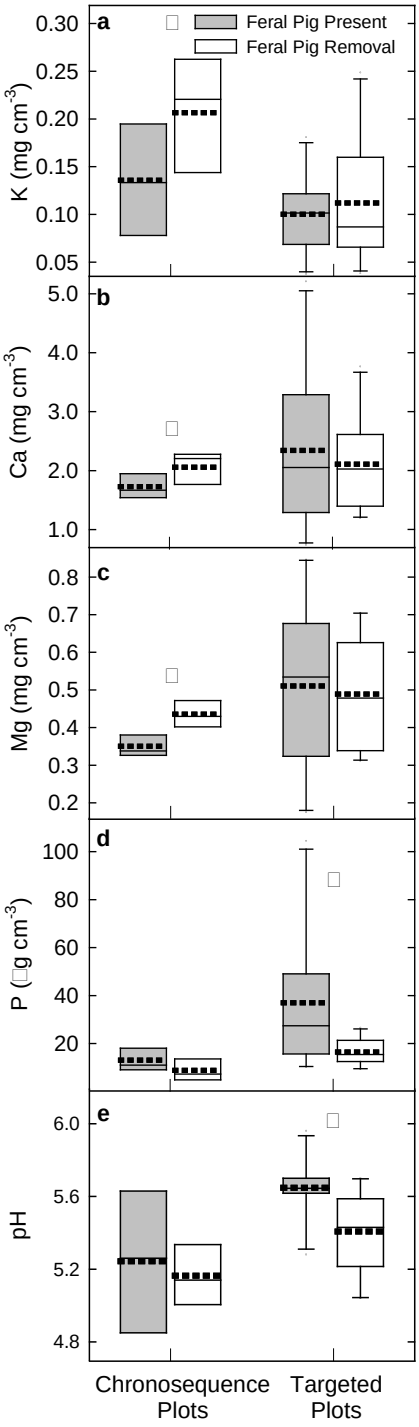

Figure 2.3 Extractable (a) K, (b) Ca, and (c) Mg increased in the chronosequence plots, while (d) extractable P and (e) soil pH decreased in the targeted plots following feral pig removal. Whiskers indicate 10% and 90% values for the targeted plots (no whiskers are presented for chronosequence plots due to small sample size); dotted lines indicate mean and solid lines indicate median values; asterisks indicate significant differences ($\alpha = 0.10$)

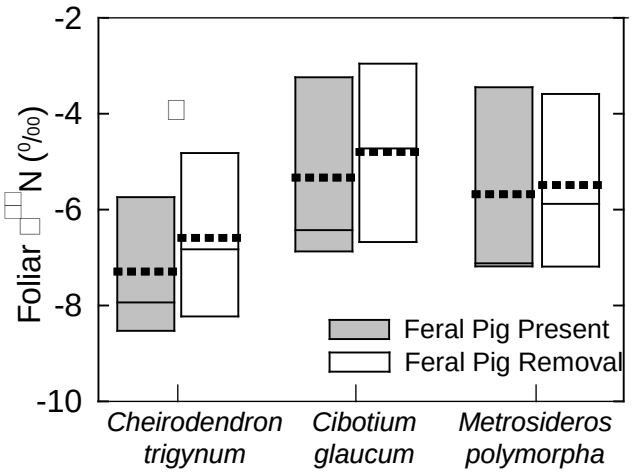

Figure 2.4 Enrichment of *Cheirodendron trigynum* foliar $\delta^{15}N$ following feral pig removal. *Cibotium glaucum* and *Metrosideros polymorpha* foliar $\delta^{15}N$ were unaffected by feral pig removal. Dotted lines indicate mean and solid lines indicate median values; asterisks indicate significant differences ($\alpha = 0.10$)

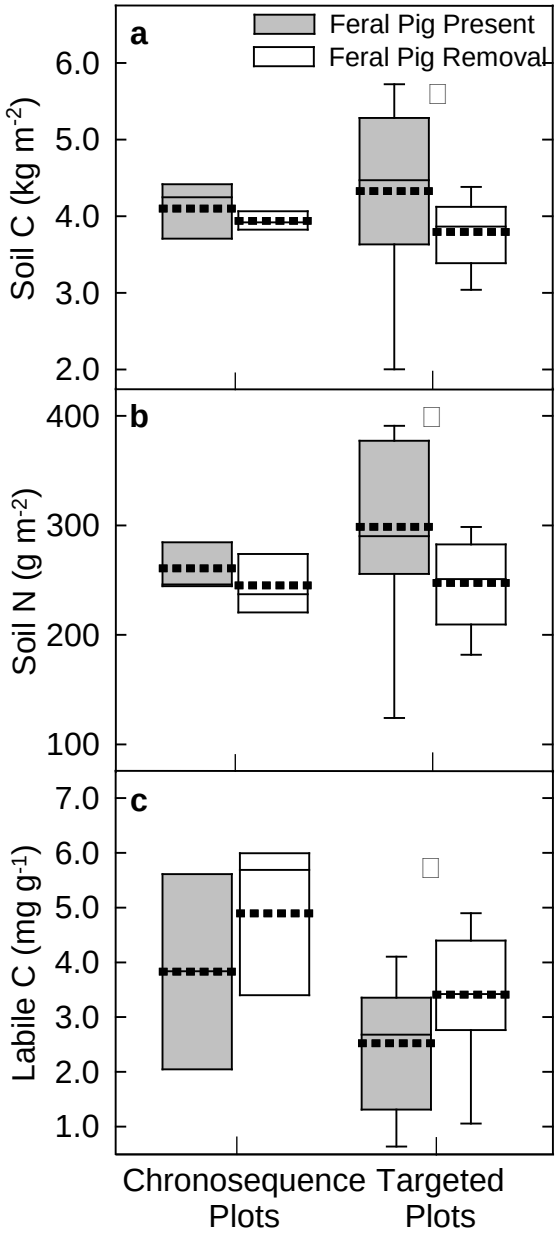

Figure 2.5 Decreases in (a) mineral soil C and (b) mineral soil N; and increase in (c) labile C following feral pig removal in the targeted plots. Whiskers indicate 10% and 90% values for the targeted plots (no whiskers are presented for chronosequence plots due to small sample size); dotted lines indicate mean and solid lines indicate median values; asterisks indicate significant differences ($\alpha = 0.10$)

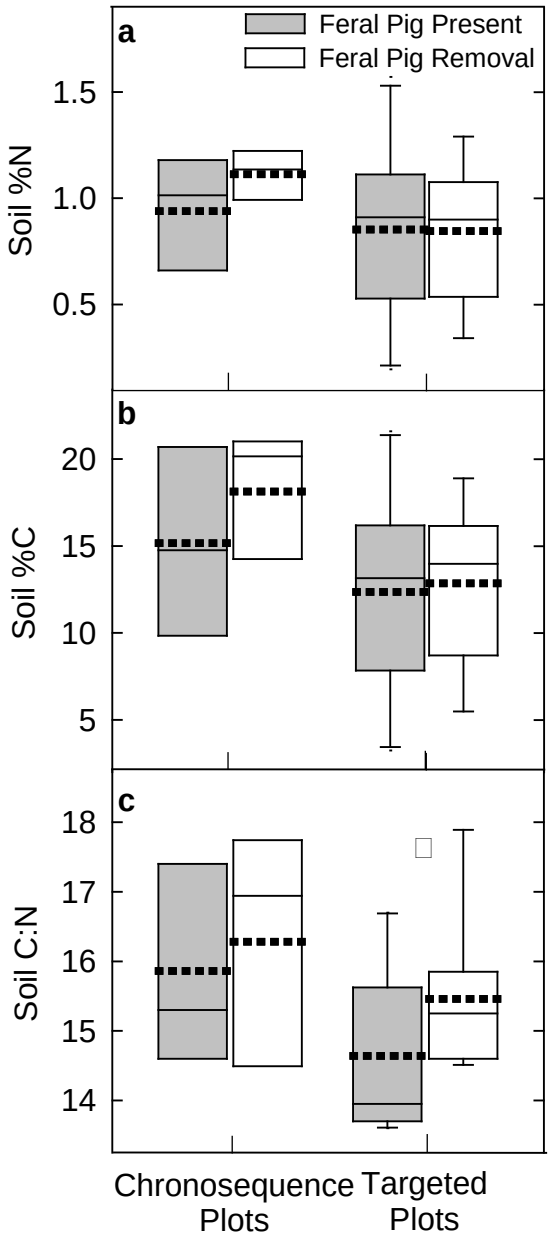

Figure 2.6 Feral pig removal did not impact (a) % N or (b) % C, but increased (c) C:N in the targeted plots. Whiskers indicate 10% and 90% values for the targeted plots (no whiskers are presented for chronosequence plots due to small sample size); dotted lines indicate mean and solid lines indicate median values; asterisks indicate significant differences ($\alpha = 0.10$)

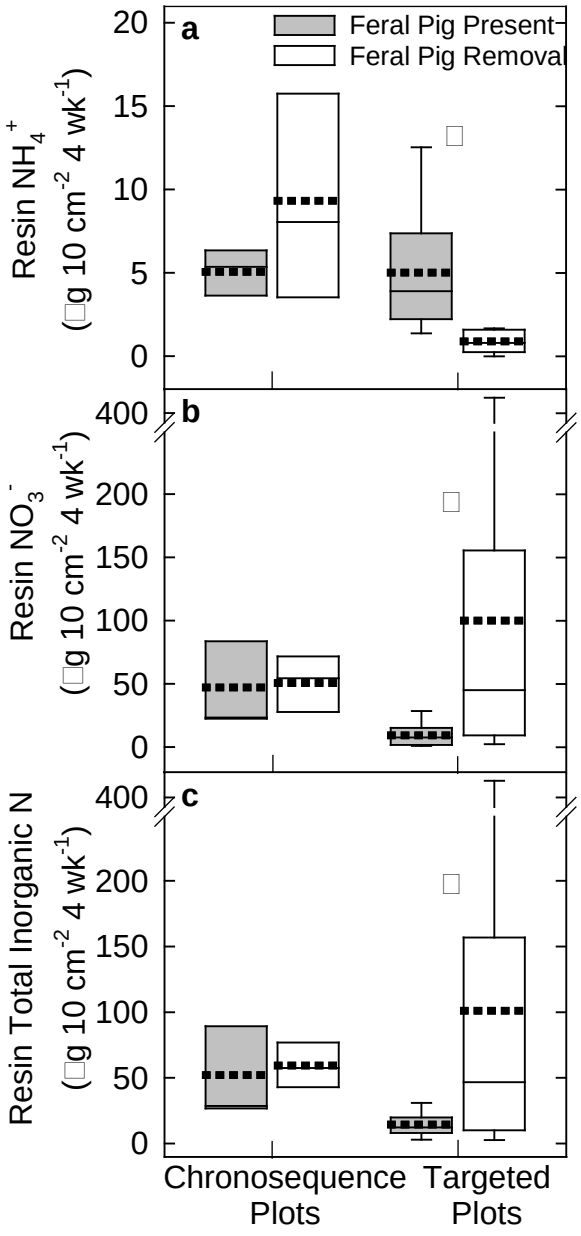

Figure 2.7 Feral pig removal resulted in a significant decrease in (a) resin available NH4+ and significant increases in (b) resin available NO3- and (c) total resin available inorganic N in targeted plots. Whiskers indicate 10% and 90% values for the targeted plots (no whiskers are presented for chronosequence plots due to small sample size); dotted lines indicate mean and solid lines indicate median values; asterisks indicate significant differences ($\alpha = 0.10$)

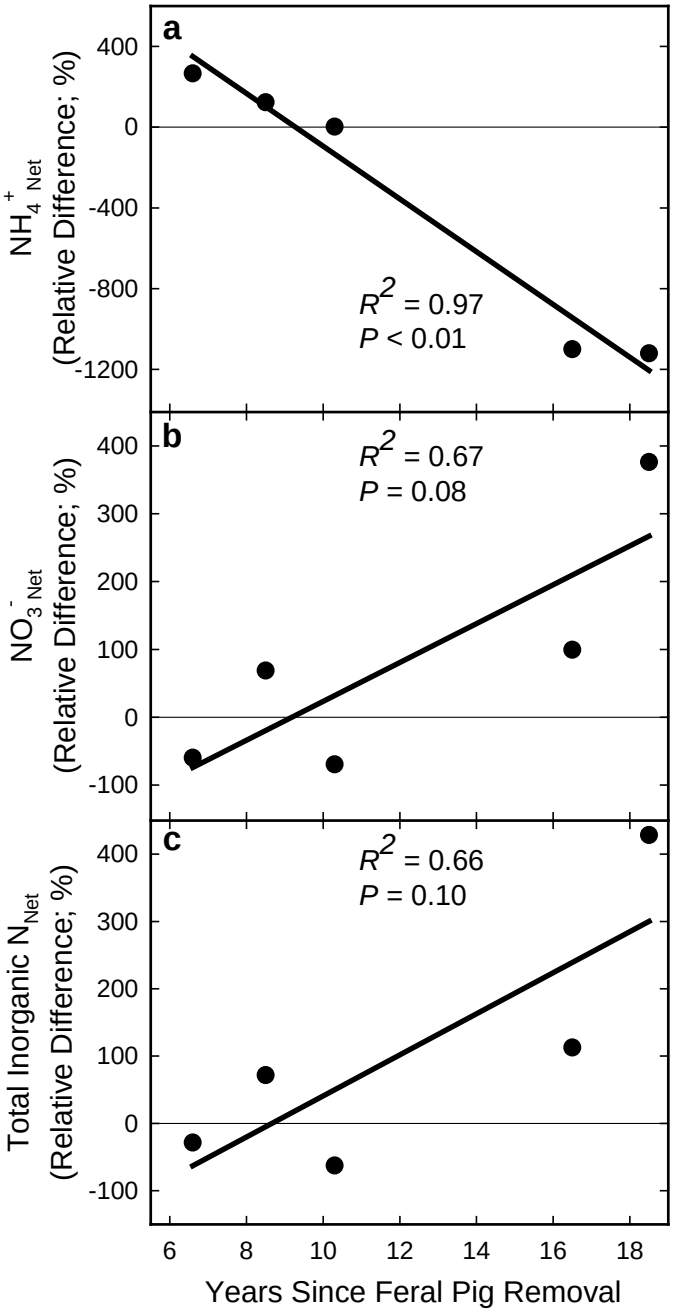

Figure 2.8 The relative difference in (a) net ammonification between paired sites was negatively related to increasing time since feral pig removal across the chronosequence plots. The relative differences in (b) net nitrification and (c) total net inorganic N mineralization between paired sites was positively related to increasing time since feral pig removal

Discussion

Soil Structure

The observed changes in several soil properties following feral pig removal support the hypothesis that this common management approach improves soil structure. Specifically, bulk density was 28% and 18% lower, VWC was 12% and 20% lower, and water-filled pore space was 7% and 21% lower with feral pig removal in the chronosequence and targeted plots, respectively. Additionally, porosity increased 5% with feral pig removal across the chronosequence. The changes in these soil properties suggest improvements in soil aggregate stability, which is vital for soil productivity and environmental quality by providing resistance to erosion, and adequate pore space for gas exchange and movement of water and nutrients (Amezketa 1999).

Soil aggregates form when exchangeable cations on soil mineral particles (i.e. soil colloids) bond with SOM particulates which bond to additional cation/particle structures (Bronick and Lal 2005). Soil aggregates are stabilized by a combination of multiple factors including, but not limited to, SOM, especially the labile C pool (Amezketa 1999), exchangeable cations, plant roots and symbionts, soil fauna, and soil moisture (Bronick and Lal 2005). In Andisols, where soil aggregates are dominated by aluminum-humus complexes and, therefore contain high SOM (Nanzyo 2002), increases in labile C and extractable cations, especially divalent Ca^{2+}, can further promote flocculation and cementation of cation/particle structures and form more stable soil aggregates (Brady and Weil 2010). Here, following feral pig removal in the chronosequence plots, extractable Ca, K, and Mg increased by 19%, 52%, and 24%, respectively, which likely contributed to lower bulk density, higher porosity, and enhanced soil structure. In the targeted plots, feral pig removal increased labile C 35% which contributed to greater soil aggregate stability, specifically, a 34% increase in WSA.

Soil aggregate stability could be diminished by feral pig digging, rooting and wallowing that can physically break apart soil macro-aggregates and expose greater SOM surface area to oxidation and decomposer microbes (Craswell and Lefroy 2001), further reducing SOM and subsequent aggregate formation and stabilization. Here, breakdown of soil aggregates by feral pig disturbance increased water-filled pore space and VWC, which could enhance leaching of aggregate stabilizing cations and labile C. Interestingly, in the feral pig removal targeted plots, WSA increased despite decreased SOC and SON storage (12% and 17%, respectively, and

driven almost exclusively by decreased bulk density), which highlights the importance of the increased labile C as an integral soil C pool that forms and stabilizes soil aggregates.

My observed improvements in soil structure following feral pig removal align with a similar decrease in bulk density found after 7 years of feral pig exclusion from montane wet forests in Hawai‘i (Vtorov 1993). In contrast, decreased soil bulk density was observed with wild boar disturbance in the Hapludands and Udivitrands of Patagonia, Argentina (Barrios-Garcia, Classen, and Simberloff 2014). Contradictions between results found in this current study and in Barrios-García et al. (2014) can be partially attributed to differences in duration of feral pig disturbance (~12 years vs. ~200 years in Hawai‘i), which likely did not allow time for repeated soil disturbances to elicit changes in soil properties (Barrios-Garcia, Classen, and Simberloff 2014). The observed reductions in bulk density, VWC, and water-filled pore space, and increase in porosity in this current study show that feral pig removal can lead to an increase in oxygen diffusion that can stimulate soil microbe activity and nutrient productivity in Hawaiian montane forests (Schuur, Chadwick, and Matson 2001; Schuur and Matson 2001).

Soil Nutrient Availability

Observed changes in several soil properties support the hypothesis that feral pig removal can enhance soil nutrient availability. Across the chronosequence plots, feral pig removal increased extractable Ca, K, and Mg. Additionally, % C, % N, and labile C were 19%, 18%, and 28% greater, respectively, across four of the five feral pig exclosures. Extractable P, however, was on average 44% and 55% lower with feral pig removal in the chronosequence and targeted plots, respectively. Lower extractable P concentrations following feral pig removal could result from a combination of several causes: loss of P input from feral pigs; accelerated P fixation by Al and Fe oxides as pH decreased; increased P uptake by recovering vegetation; greater leaching due to increased porosity; or decreased bulk density which reduces the amount of parent material per unit volume of soil.

My N mineralization results reflect the consequences of improved soil structure following feral pig removal. For instance, increasing time since feral pig removal had both a positive linear relationship with net nitrification and a negative linear relationship with net ammonification. Likewise, resin available NH_4^+ decreased while NO_3^- increased in the feral pig removal targeted plots. Elevated nitrification following feral pig removal was reflected in

enriched *C. trigynum* foliar $\delta^{15}N$ as increased N cycling likely created a more open N cycle and enriched $\delta^{15}N$ product for plant uptake (Evans 2001). These results suggest that nitrifying soil microbes capitalize on increased porosity, decreased water-filled pore space and a greater supply of labile C. Similar to the impacts of feral pig disturbance in this current study, grazing by large herbivores on clay soils in salt marshes in the Netherlands increased soil moisture, reduced redox potentials, and reduced N mineralization rates (Schrama et al. 2012). Alternatively, lower NO_3^- in feral pig disturbed soil could result from elevated soil VWC and water-filled pore space, and reduced porosity, as these soils have low hydraulic resistance and can readily leach NO_3^- (Lohse and Matson 2005).

My results contrast with increases in soil nutrient availability found following wild boar disturbances in both their native and introduced ranges. In their native range within Swiss hardwood forests, wild boar rooting and mixing of organic matter through the soil profile in the relatively SOM-poor sandy-loam soil in the cool and dry forest was proposed to stimulate microbial activity, enhance SOM decomposition, and increase soil % C and % N (Wirthner et al. 2012). In their introduced range of pine-hardwood forests in Texas, wild boar disturbance was suggested to increase soil nutrient availability by aerating soil and accelerating SOM decomposition and N mineralization (Siemann et al. 2009). However, in this current study in warm and wet Andisols with high SOM, physical soil disturbance by feral pigs could likewise lead to SOM decomposition, but a concurrent loss of soil structure and an elevation in VWC and water-filled pore space likely limits gas exchange and inhibits the aerobic production and availability of soil nutrients (Schuur, Chadwick, and Matson 2001; Schuur and Matson 2001).

Recovery of Soils and Vegetation

Improvements in soil structure and increases in nutrient availability following feral pig removal in these study sites could be an underlying mechanism for an overall increase in the density and abundance of understory plants (Cole and Litton 2014). A resurgence of soil fauna following feral pig removal was previously documented in this same forest type (Vtorov 1993), which likely contributed to accelerated SOM decomposition, N mineralization and availability of soil aggregate stabilizing cations. Recovering vegetation likely capitalized on increased nutrient availability and further stabilized soil aggregates via fine root and hyphal growth.

Vegetative recovery across the chronosequence plots was not restricted to native species, however, as stem density of the highly invasive *Psidium cattleianum* Sabine increased as much as five fold following feral pig removal in the sites where it was present at the time of feral pig removal, likely as a result of the release of top-down control with the removal of feral pigs (Cole and Litton 2014). The combination of improved soil structure and nutrient availability with increasing nonnative plant establishment following feral pig removal highlights that underlying soil processes likely play a large role in competitive dynamics between native and nonnative plants following feral pig removal, and supports the fluctuating resource availability hypothesis of invasibility (Davis, Grime, and Thompson 2000). The spread of nonnative plants after feral pig removal documented here and with ungulate removal elsewhere in Hawai‘i (Weller et al. 2011; Thaxton et al. 2010; Cabin et al. 2000; Stone, Cuddihy, and Tunison 1992; Scowcroft and Hobdy 1987; Kellner et al. 2011) highlights the need for active vegetation management following nonnative ungulate removal. Given the ability of nonnative plants to take advantage of increased resource supply compared to the conservative nutrient use of native plants (Funk and Vitousek 2007), the increase in the cycling and availability of soil nutrients with feral pig removal observed here suggests that management strategies to reduce nutrient availability following the removal of nonnative ungulates may favor native species.

Data Limitations

Across the chronosequence, statistical analyses revealed no differences in several soil properties. Inability to detect significant impacts for these variables, if they existed, could have been due to several factors. First, the digging and foraging behavior of feral pigs is not uniform across a landscape. Feral pig disturbance can vary based on availability of food sources (Lincoln 2014; Anderson and Stone 1994; Diong 1982) and soil moisture and texture (Caley 1993; Elledge et al. 2012), and therefore, is not evenly distributed throughout a forest. Such preferential behavior by feral pigs could limit detectability of their impacts on soils in observational studies (Siemann et al. 2009). Still, despite low sample size and non-random disturbances by feral pigs, there was general agreement between results from the chronosequence and targeted plots, which together provide what I consider to be robust evidence to suggest that feral pig removal improves soil structure and nutrient availability.

A second limiting factor in this study was the small sample size (n = 5) in the chronosequence plots due to a limited set of existing exclosures from the past. My small sample size required a conservative Wilcoxon Signed-Rank test that reduces the likelihood of Type II errors. Further, it is possible that I collected samples from too few plots (n = 4) within each site to adequately characterize each site and sufficiently control for the inherent heterogeneity of soil properties and feral pig disturbances (see Davidson and Hewitt 2014). For example, in one feral pig present plot in the chronosequence (8.5 years), resin available NO_3^- was an order of magnitude greater than the other three plots, thereby skewing the mean value for the site and greatly influencing the ability to detect significant differences. While more plots within each site would not increase the overall sample size, it could potentially diminish skew created by an exceedingly high or low measurement.

Conclusions

This study documented that feral pig removal from tropical montane wet forests on the Island of Hawai‘i impacted several soil properties and indicates that this land management technique improves soil structure and increases nutrient availability. Specifically, results showed that feral pig removal increased extractable cations, labile C, WSA, porosity, *C. trigynum* foliar $\delta^{15}N$, and resin available NH_4^+, while decreasing extractable P, bulk density, VWC, water-filled pore space, resin available NO_3^-, and pH. Additionally, increasing time since feral pig removal was related to decreasing ammonification and increasing nitrification. Despite the inherent heterogeneity of soils and feral pig disturbance that challenges standard sampling schemes, these results suggest that recovery of both native and nonnative vegetation following nonnative ungulate removal (Cole and Litton 2014) is at least partially the result of alterations to underlying soil properties. These soil characteristics potentially drive vegetation responses to the removal of nonnative ungulates, but to date had received little attention in the scientific literature.

CHAPTER 3

Removal of nonnative feral pigs from Hawaiian tropical montane wet forests increases belowground carbon flux without changing soil carbon storage

Abstract

Nonnative ungulate removal from fenced exclosures is a common management practice globally to benefit native ecosystems. Relative to the impacts of this practice on vegetation communities, little is known about the response of belowground ecological processes, particularly soil carbon (C) dynamics, to nonnative ungulate removal. Here, I quantified the impacts of nonnative feral pig (*Sus scrofa*) removal on soil C pools (forest floor and mineral soil) and fluxes (litterfall, F_L; soil-surface CO_2 efflux, F_S; and total belowground C flux, TBCF) in Hawaiian tropical montane wet forests using paired sites inside and outside of an established chronosequence of five management units ranging in age from 6.6 – 18.5 years since removal. Overall, C flux in F_S and TBCF increased by 18% and 24%, respectively, while F_L did not change with feral pig removal. Additionally, F_S and TBCF showed positive linear relationships with increasing time since feral pig removal (i.e., the longer ungulates were excluded, the larger the differences inside vs. outside of exclosures). Despite large changes in the input of C into and out of soils, soil C pools did not vary following feral pig removal. These results suggest that feral pig removal increases belowground C cycling, likely via previously documented changes to soil physical and chemical properties and understory vegetation following feral pig removal in this system, without impacting soil C storage. Such changes in belowground ecosystem processes are important to understand in the context of rising atmospheric CO_2 levels and global climate change that can be accentuated or ameliorated by management of invasive species.

Introduction

Ecosystem processes are impacted by nonnative species invasions globally (R. N. Mack et al. 2000; Vitousek et al. 1996; M. C. Mack and D'Antonio 1998; Ehrenfeld 2003), with negative impacts to local and national economies (Pejchar and Mooney 2009; Pimentel et al. 2000). Nonnative ungulates can act as ecosystem engineers (Jones, Lawton, and Shachak 1997; Keuroghlian and Eaton 2009; Sandom, Hughes, and Macdonald 2013), and alter soil chemical (Siemann et al. 2009; Krull et al. 2013; Kardol et al. 2014; Hata et al. 2014; Chapter 2), physical (Vtorov 1993; Beever, Huso, and Pyke 2006; Kardol et al. 2014; Chapter 2) and biological (Vtorov 1993; Kaller and Kelso 2006; Wirthner et al. 2011; Mohr, Cohnstaedt, and Topp 2005) properties. Changes in the belowground ecosystem, in particular, can have subsequent impacts on plant community composition (Stohlgren, Schell, and Heuvel 1999; Knauf et al., *In review*), often resulting in the local extirpation of native taxa (Campbell and Long 2009; Spear and Chown 2009; Nuñez, Bailey, and Schweitzer 2010; Oduor, Gómez, and Strauss 2010). Consequently, nonnative ungulate removal is an increasingly common management strategy globally for the protection and recovery of native ecosystems (Courchamp, Chapuis, and Pascal 2003; Tanentzap et al. 2009; Wright et al. 2012; Cole and Litton 2014; Hess 2016). However, the belowground impacts of nonnative ungulate invasions, and their removal, remain understudied. This is of particular importance given the need for a better understanding of the impacts of nonnative invasive species on ecosystem carbon (C) dynamics (Peltzer et al. 2010) in the context of rising global terrestrial carbon dioxide (CO_2) emissions and global climate change (IPCC 2014).

Most of the C in terrestrial ecosystems, approximately 2,300 Pg C, resides in the top 2 m of the soil profile (Jackson et al. 2017), with tropical forests containing more soil C than temperate and boreal forests combined (Jobbagy and Jackson 2000). Nonnative feral pigs (*Sus scrofa* Linnaeus, 1758) have invaded tropical forest ecosystems globally (Barrios-Garcia and Ballari 2012), and are now present in nearly all forest habitats. Because feral pigs can root and mix soils to depths of ~25 cm (Lacki and Lancia 1983), the large fraction of total soil C located in the upper 20 cm of forest soils globally (Jobbagy and Jackson 2000) is particularly vulnerable to the impacts of feral pigs. This is important because soil C storage is determined by the balance of soil C inputs and outputs, and soil disturbances and changes in vegetation following feral pig invasions (Campbell and Long 2009; Spear and Chown 2009; Barrios-Garcia and Ballari 2012;

Cole et al. 2012; Cole and Litton 2014) have the potential to alter C inputs to forest soils via litterfall (F_L) and total belowground C flux (TBCF; C flux to belowground by plants to support root exudates and to the growth and maintenance of roots and mycorrhizae, (Raich and Nadelhoffer 1989; Nadelhoffer, Raich, and Aber 1998; Giardina and Ryan 2002; Litton, Ryan, and Knight 2004)), as well as C output from forest soils via soil-surface CO_2 efflux (F_S; 'soil respiration') (Metcalfe, Fisher, and Wardle 2011).

Given the large scale of feral pig invasions across nearly all continents and oceanic islands, nonnative feral pigs may already be influencing terrestrial carbon balance, with impacts on atmospheric CO_2 levels. In addition, ungulate herbivores likely have distinct impacts from those that root in and disturb soils. In Switzerland, wild boar (*Sus scrofa* in native range) grubbing increased F_S by 23% compared to adjacent, ungrubbed sites over three years (Risch et al. 2010), and this change was attributed to the incorporation of organic material from the surface litter layer into deeper mineral soil with grubbing and increased SOM decomposition, but also changes to soil gas diffusion, and fine root and microbial biomass and activity.

While wild boar activity was shown to increase F_S in Swiss forests, Risch et. al. (2010) did not investigate fluxes of C to belowground that could potentially offset increased F_S resulting from wild boar activity (i.e., F_L and TBCF). Prior studies have shown that increased F_S in the context of rising temperatures did not alter soil C storage because of a concomitant increase in the flux of C to belowground via F_L and TBCF (Giardina et al. 2014). No study to my knowledge has investigated the impact of feral pig presence or removal on cumulative soil C cycling and storage, which is crucial for understanding soil C dynamics (Kuzyakov 2011).

Prior research has shown mixed impacts of feral pigs on soil C storage for mineral soil C (C_{Soil}) and litter layer C (C_{Litter}) pools. For example, feral pig activity increased C_{Soil} in Tennessee high elevation beech gaps (Lacki and Lancia 1983), yet had no effect on C_{Soil} under oak canopies or grasslands on Santa Cruz Island, California (Moody and Jones 2000). Elsewhere, C_{Litter} was reduced by feral pigs due to mixing of the litter layer into the soil profile in Texan mixed pine-hardwood forest (Siemann et al. 2009), Tennessee deciduous forests (Singer, Swank, and Clebsch 1984) and Australian lowland tropical rainforests (Taylor, Leung, and Gordon 2011). Conversely, no changes in soil C pools were seen in Australian highland tropical rainforests (Mitchell et al. 2007). Noticeably absent from these studies was information on the impacts of

feral pigs on belowground soil C cycling in the context of C inputs and outputs, which is needed to mechanistically understand observed changes in soil C storage.

Feral pig introduction to the Hawaiian Islands first occurred between 1000 and 1200 AD with the arrival of ancient Polynesians who brought with them a smaller Polynesian variety of *Sus scrofa* (Wehr, Hess, and Litton, I*n press*). Subsequent arrivals to Hawai‘i by Captain James Cook in 1778-1779, and later European settlers, introduced the larger European wild boar and domesticated lineages of swine, which interbred with the Polynesian variety to produce the feral pigs found throughout the Hawaiian Islands today, as well as on many other Pacific Islands (Linderholm et al. 2016; Wehr, Hess, and Litton, *In press*). Here, I use the term “feral pig” to refer to the mixed Polynesian and European pigs that have proliferated and degraded native ecosystems throughout the Pacific Island Region (Steven C. Hess 2016; Wehr, Hess, and Litton, *In press*), and prompted the construction of fenced management units (i.e., ungulate exclosures) around areas of high conservation value (Hess 2016).

In this study, the impacts of feral pig removal on soil C pools and fluxes were examined utilizing a previously established model study system located along an 18.5 year chronosequence of feral pig exclosures in Hawaiian tropical montane wet forests (Cole and Litton 2014; Chapter 2). Prior work in this study system documented that native understory stem density, species richness, and presence of ground-rooted woody plants were much higher within exclosures than in surrounding forest with feral pigs, while canopy vegetation was constant (Cole and Litton 2014). In addition, feral pig removal along this chronosequence decreased soil bulk density and water content, and increased soil aggregation, porosity, nutrient availability, and labile C content (Chapter 2). Overall, these data indicate improved soil physical and chemical properties with feral pig removal. As a result of documented changes in vegetation and soil properties with feral pig removal in this ecosystem, I hypothesized an increase in inputs of C to soils via F_L and TBCF that would be balanced by increased soil C output via F_S, with no overall change in soil C storage. I also hypothesized that changes in soil C inputs and outputs would increase with time since feral pig removal. These hypotheses were tested by quantifying soil C pools (C_{Soil} and C_{Litter}) and fluxes (F_S, F_L, and TCBF) inside and outside of five feral pig removal management units arrayed across an 18.5 year chronosequence of ungulate removal where overstory canopy, substrate type and age, climate and disturbance history are relatively constant.

Methods

Study Sites

The study was conducted between August 2010 and December 2012 along a chronosequence of five feral pig exclosures ranging from 6.5 to 18.5 years since feral pig removal on the East flank of Mauna Loa Volcano on the Island of Hawai‘i (Cole and Litton 2014; Chapter 2). Estimated feral pig densities in surrounding forest range from 0.6 to 16.3 animals/km^2 (Scheffler et al. 2012). Study sites are located between 1,140 and 1,370 m.a.s.l. Mean annual temperature and precipitation range from 14.4 to 15.9 °C and 2,910 to 3,985 mm, respectively, across study sites with little seasonality (Giambelluca et al. 2013, 2014). All study sites are located on 2,000 – 10,000 year-old, tephra-derived Andisols of two closely related series: Eheuiki (medial, ferrihydritic, isothermic Typic Hydrudands) and Puaulu (medial over ashy, aniso, ferrihydritic over amorphic, isothermic Aquic Hapludands) (NRCS 2010). These soil series are characterized by deep, moderately well drained soils formed in basic volcanic ash deposited over basic lava with slopes of 2-5% (NRCS 2010). All study sites are located in *Metrosideros polymorpha* Gaudich. (overstory tree)/*Cibotium* spp. (midstory tree fern) tropical montane wet forest (Wagner, Herbst, and Sohmer 1990) with exclusively native canopy vegetation. Canopy species composition, stand density, and basal area do not vary inside vs. outside of exclosures (Cole and Litton 2014).

Along the chronosequence, pairs of study sites were established inside and outside of each of the five exclosures. Each study site consisted of four circular 18 m radius (1,018 m^2) sampling plots located > 70 m from fence lines and > 140 m from each other. In each sampling plot, I quantified soil C pools (C_{Litter}, and C_{Soil} down to 50 cm) and annual soil C fluxes (F_S, F_L, and TBCF), and averaged across plots for a single study site value. Intensive sampling in plots inside and outside of the second oldest exclosure (16.5 years without feral pigs vs. feral pigs present) revealed no difference in fine root (C_{root}) biomass, so this variable was not quantified across the entire chronosequence.

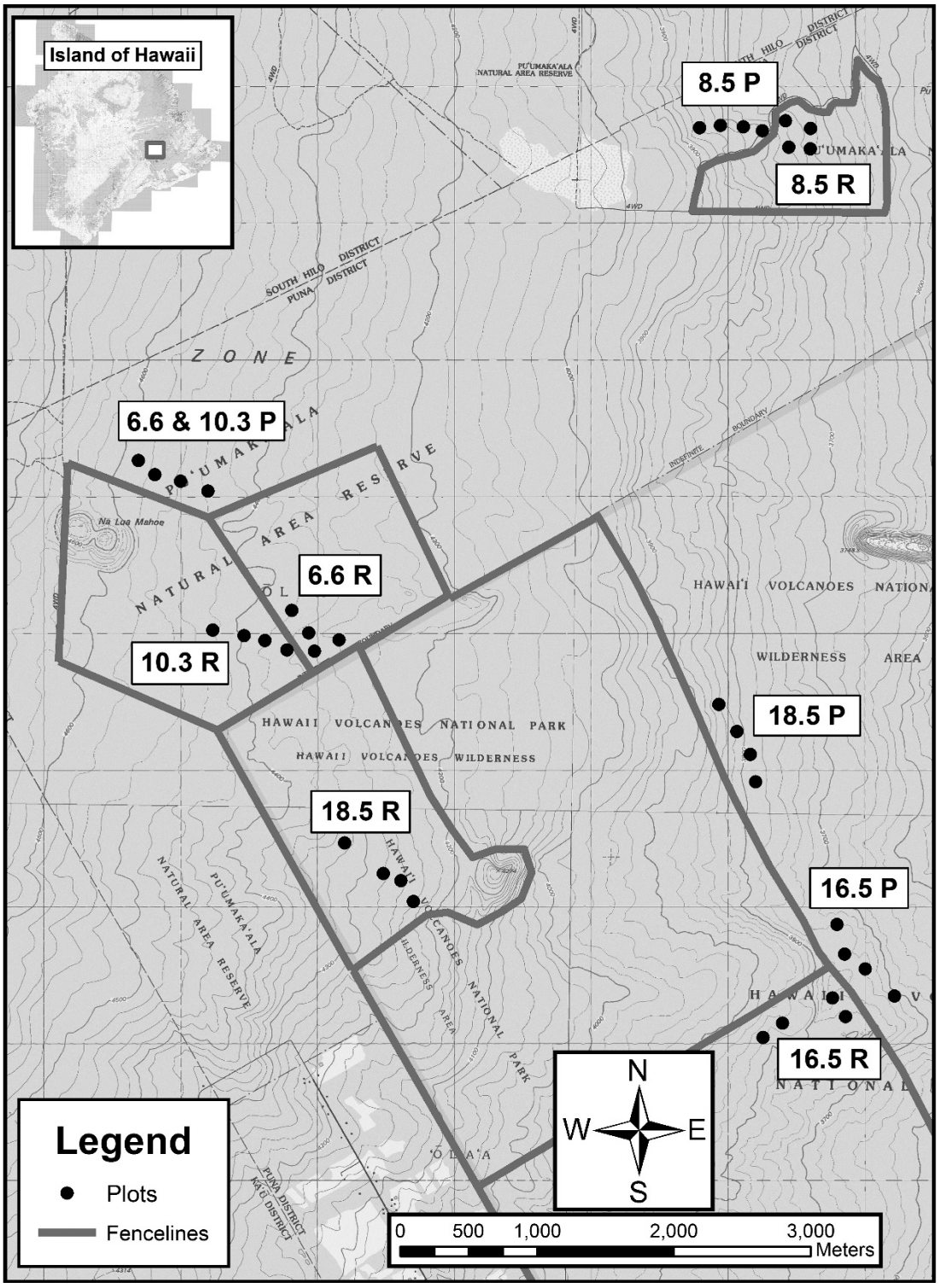

Figure 3.2 Study site locations inside and outside of feral pig exclosures on the East slope of Mauna Loa Volcano, Island of Hawai‘i. Paired study sites are labeled by years since feral pig removal and feral pig presence (P) or feral pig removal (R)

Soil Carbon Pool

Mineral soil C (C_{Soil}; g C m^{-2}) was quantified in each plot with incremental soil cores (0-10 cm, n = 10; 10-30 cm, n = 5; 30-50 cm, n = 3) to a maximum depth of 50 cm in the summer of 2012. Soil samples were collected at ten uniformly arrayed locations within a 9 m radius centered on each plot, and composited by plot. Surface mineral soil (0-10 cm depth, which included the Oa horizon and mineral soil) was collected at all ten locations while the incremental depths were randomly assigned. Surface soil was collected using a 10 cm tall x 5.1 cm diameter soil corer. Soil from the 10-30 and 30-50 cm depths was collected using a 4.75 cm diameter soil corer. To ensure consistent soil core volumes and minimize soil compaction, each core increment was extracted sequentially. Roots and rocks > 0.6 cm in each composited sample were removed by hand and sieve, and soils were weighed and homogenized for analyses. Homogenized sub-samples of field-moist soil were oven-dried at 70°C to a constant mass and passed through a 2 mm (#10) sieve. A representative sub-sample was ball-milled, passed through a 0.5 mm (#40) sieve, and analyzed for %C with a Costech Elemental Analyzer (Costech Analytical Technologies Inc., Valencia, CA) at the University of Hawai‘i at Hilo Analytical Laboratory. C_{Soil} (g C m^{-2}) for each core increment was calculated as:

$$C_{Soil} = \%C_{Soil} \times BD \times L \times 10000 \qquad \text{[Eq. 1]}$$

Where $\%C_{Soil}$ = percentage of C in the core increment (g C g^{-1} soil); BD = core increment bulk density (g soil cm^{-3}; Chapter 2); and L = length of the core increment (cm).

Forest Floor Carbon

Forest floor C (C_{Litter}; g C m^{-2}) was determined by collecting the litter layer (O_i and O_e horizons) within a 0.17 m^2 frame placed over the ten soil core locations. All litter was collected down to mineral soil or, in most cases, the thick root mat that typically occurs in the O_a horizon in these forests. The litter was composited by plot, oven-dried at 70°C to a constant mass in a forced-air oven and weighed. The entire sample was homogenized on a large Wiley mill, and a representative sub-sample was then ball-milled, passed through a 0.5 mm (#40) sieve, and analyzed for %C with a Costech Elemental Analyzer (Costech Analytical Technologies Inc., Valencia, CA) at the University of Hawai‘i at Hilo Analytical Laboratory. C_{Litter} was calculated as:

$$C_{Litter} = M_{Litter}/\text{Area} \times \%C \quad \text{[Eq. 2]}$$

Where M_{Litter} = litter dry weight (g); Area = total area of the litter trays (m^2); and %C = percentage of C in the litter layer (g C g^{-1} litter).

Annual Aboveground Litterfall

Annual aboveground litterfall (F_L; g C m^{-2} yr^{-1}) was quantified via monthly litterfall collections in each plot throughout 2011 (12 total collections). Litterfall was collected with eight 0.17 m^2 litter traps per plot, and composited by plot. Collected material was oven dried to a constant mass in a forced-air oven at 70°C and weighed. The entire sample was homogenized on a large Wiley mill, and a representative sub-sample was then ball-milled, passed through a 0.5 mm (#40) sieve, and analyzed for %C concentration (C_{FL}) with a Costech Elemental Analyzer (Costech Analytical Technologies Inc., Valencia, CA) at the University of Hawai‘i at Hilo Analytical Laboratory. Annual plot F_L was calculated as:

$$F_L = \Sigma\ (M_{Litter} / \text{Area}) \times C_{FL} \times \#_{days}/365 \quad \text{[Eq. 3]}$$

where M_{Litter} is the monthly litterfall (g), Area is the total surface area of the litter traps, C_{FL} is the litterfall %C concentration (g C g^{-1} litter); and $\#_{days}$ is the total number of days that the litter traps were deployed.

Annual Soil-surface CO_2 efflux

Annual soil-surface CO_2 efflux (F_S; g C $m^{-2}yr^{-1}$) was calculated from instantaneous F_S measurements (µmol CO_2 $m^{-2}s^{-1}$) taken in each plot in the Fall of 2010 and the Summer of 2011 between 8:00 am and 4:30 pm on days without rainfall. There is no diel cycle to F_S in these forests so instantaneous measurements throughout the day can be scaled to annual flux (Litton et al. 2011). Twelve evenly spaced 20 cm diameter x 10 cm tall PVC soil collars were installed within a 9 m radius plot to a depth of 4 cm, and left in the soil for at least 1 month prior to initial measurements. Instantaneous F_S was measured at each collar with a closed chamber Li-8100A Automated Soil CO_2 Flux System (Li-Cor Biosciences, NE). Each collar measurement was the average of two sequential 70 second observations separated by a one minute observation delay in which the chamber opened to allow free air circulation to the atmosphere. Immediately prior to each observation, a 20 second “deadban” was implemented to allow gases to equilibrate after

closing the chamber. If the two sequential observations differed by more than 15%, additional observations were conducted until measurements were within 15% of each other. Instantaneous measurements of F_S were averaged across all collars within each plot to calculate a plot mean F_S. Because, F_S in these ecosystems varies seasonally but not on diel scales (Litton et al. 2011), site mean F_S was then estimated by first averaging plot F_S across all four plots in a study site, and then averaging F_S from the Fall 2010 and Summer 2011 measurements. These averages where then multiplied by 378.77 g C μmol CO_2^{-1} s yr^{-1} to convert instantaneous measurements to annual F_S (g C m^{-2} yr^{-1}).

Annual Total Belowground Carbon Flux (TBCF)

Annual total belowground C flux (TBCF; g C m^{-2} yr^{-1}) in the feral pig removal sites was estimated via mass balance based on the assumption of non-steady state conditions where there are appreciable or unknown changes in soil C pools over time (e.g., rapidly aggrading forests recovering from disturbances) (Giardina and Ryan 2002). Of the basic soil C pools used to calculate TBCF (mineral soil, forest floor litter, and root biomass), two studies in contrasting ecosystems found that changes in forest floor litter and coarse root C had the greatest impact on TBCF (Giardina and Ryan 2002; Litton, Ryan, and Knight 2004). Coarse root C is a direct function of aboveground C (Mokany, Raison, and Prokushkin 2006), and because feral pig removal across the chronosequence did not alter woody canopy stem density or basal area (Cole and Litton 2014), I assumed no change in coarse root C storage over time. Therefore, TBCF was calculated as:

$$TBCF = F_S - F_L + \Delta C_{Litter} \quad \text{[Eq. 4]}$$

Where F_S was annual soil-surface C efflux, F_L was annual litterfall C, and ΔC_{Litter} was the annualized change in C_{Litter} following feral pig removal (i.e., absolute difference in C_{Litter} between paired sites divided by the age of the exclosure).

Because of ~200 years of feral pig invasion in this study system and the lack of baseline soil C pool values, in the feral pig present sites I assumed steady state conditions for soil C pools and TBCF was estimated via mass balance as:

$$TBCF = F_S - F_L \quad \text{[Eq. 5]}$$

Statistical Analyses

To determine if feral pig removal had a significant effect on C pools and fluxes across all study sites across the chronosequence, conservative, non-parametric one-sided Wilcoxon signed-rank tests were conducted on differences between site mean values in each pair of sites due to the small sample size (n = 5), where site mean values were an average of the four replicate plots. The effect of time since feral pig removal on soil C pools and fluxes across the chronosequence sites (n = 5) was assessed with linear regression analyses of time since removal versus the percent relative difference in site means of each variable between paired sites:

[(Feral pig removal – Feral pig present) / Feral pig present] *100 [Eq. 6]

All statistical analyses were conducted using Minitab 17 statistical software (State College, PA) with $\alpha = 0.10$ for significance given the small sample size. Treatment means ± 1 standard error (S.E.) are reported throughout.

Results

Across all study sites, feral pig removal increased annual F_S by 18%, from 1251.2 ± 89.6 to 1481.3 ± 78.5 g C m^{-2} yr^{-1} (W = 14, P = 0.03; n = 5) (Fig. 3.2b). Annual F_S ranged from 906.9 ± 97.0 to 1392.3 ± 119.3 g C m^{-2} yr^{-1} in feral pig present sites and 1274.3 ± 50.7 to 1761.1 ± 293.6 g C m^{-2} yr^{-1} in feral pig removal sites (Fig. 3.4a). Feral pig removal increased annual TBCF by 25%, from 916.3 ± 112.5 to 1143.4 ± 77.0 g C m^{-2} yr^{-1} (W = 14, P = 0.05; n = 5) (Fig. 3.2c). Annual TBCF ranged from 480.2 ± 106.7 to 1374.9 ± 77.8 g C m^{-2} yr^{-1} in feral pig present sites and 988.6 ± 79.4 to 1404.5 ± 300.4 g C m^{-2} yr^{-1} in feral pig removal sites (Fig. 3.4c). Annual F_L ranged from 254.7 ± 22.7 to 426.7 ± 24.0 g C m^{-2} yr^{-1} in feral pig present sites and 253.3 ± 15.2 to 482.5 ±65.3 g C m^{-2} yr^{-1} in feral pig removal sites (Fig. 3.4b), and did not differ across all study sites (W = 10, P = 0.30; n = 5) (Fig. 3.2a).

Across all study sites, C_{Litter} ranged from 248.0 to 538.0 g C m^{-2} and mean treatment C_{Litter} increased 21% following feral pig removal, however this increase was not significant (W = 11, P = 0.21; n = 5; Fig. 3.3a). Soil C storage did not vary with feral pig removal at any depth (Fig. 3.3); 0 – 10 cm C_{Soil} ranged from 3695.7 to 4585.8 g C m^{-2} (W = 5, P = 0.79; n = 5; Fig. 3.3b); 10 – 30 cm C_{Soil} ranged from 2854.6 to 5189.2 g C m^{-2} (W = 7, P = 0.61; n = 5; Fig. 3.3c); and 30 – 50 cm C_{Soil} ranged 3153.2 to 4397.6 g C m^{-2} (W = 4, P = 0.86; n = 5; Fig. 3.3d).

Cumulatively, C storage down to 50 cm (C_{Litter} + C_{Soil}) ranged from 10879.3 to 14192.2 g C m^{-2} and did not vary with feral pig removal (W = 5, P = 0.79; n = 5) (Fig. 3.3e).

The relative difference in F_S between paired treatments showed a significant positive linear relationship with time since feral pig removal ($F_{(1,3)}$ = 26.04, R^2 = 0.90, P = 0.02; n = 5), increasing from a relative difference of 4% in the youngest exclosure (6.5 years since feral pig removal) to 62% in the oldest exclosure (18.5 years since feral pig removal) (Fig. 3.4d). TBCF also showed a significant positive linear relationship with time since feral pig removal ($F_{(1,3)}$ = 18.87, R^2 = 0.86, P = 0.02, n = 5), increasing from 5% in the youngest exclosure to 106% in the oldest exclosure (Fig. 3.4f). The relative difference in C_{Litter} within each pair of sites tended to increase positively with increasing time since feral pig removal, ranging from a 12% relative difference in the youngest exclosure to 117% in the oldest exclosure, but the relationship was not significant ($F_{(1,3)}$ = 4.63, R^2 = 0.61; P = 0.12, n = 5). There were no significant linear relationships between increasing time since feral pig removal and F_L ($F_{(1,3)}$ = 0.22, R^2 = 0.07, P = 0.67, n = 5; Fig. 3.4e) or C_{Soil} at any depth interval: 0 – 10 cm ($F_{(1,3)}$ = 0.02, R^2 = 0.01, P = 0.90, n = 5), 10 – 30 cm ($F_{(1,3)}$ = 1.68, R^2 = 0.36, P = 0.29, n = 5), 30 – 50 cm ($F_{(1,3)}$ = 0.80, R^2 = 0.21, P = 0.44, n = 5), and total soil C ($F_{(1,3)}$ = 1.22, R^2 = 0.29, P = 0.35, n = 5).

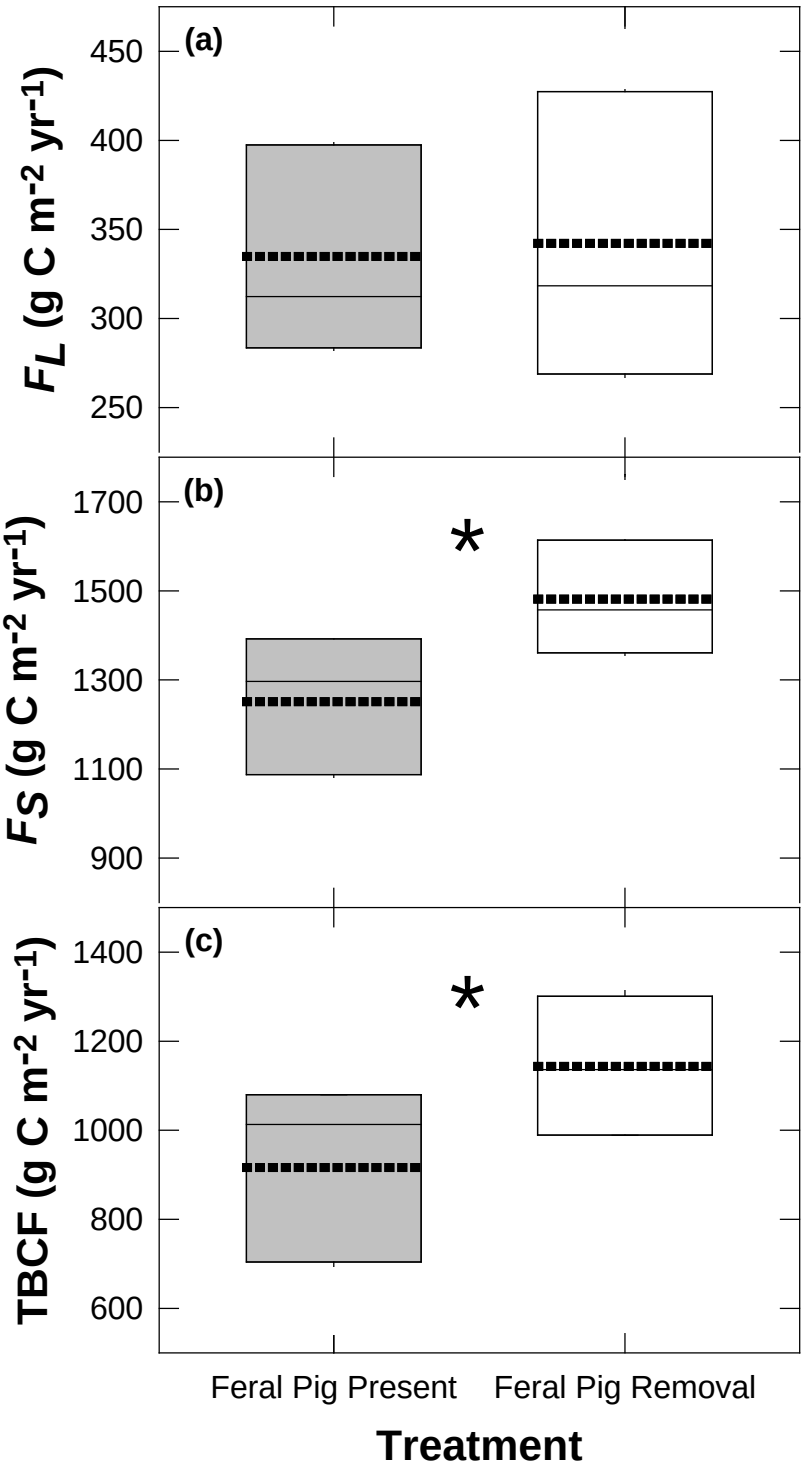

Figure 3.2 Across the chronosequence of feral pig exclosures, feral pig removal did not impact (a) F_L, but significantly increased (b) F_S and (c) TBCF. Box plot whiskers are absent due to small sample size; dotted lines indicate mean and solid lines indicate median values; asterisks indicate significant differences ($\alpha = 0.10$)

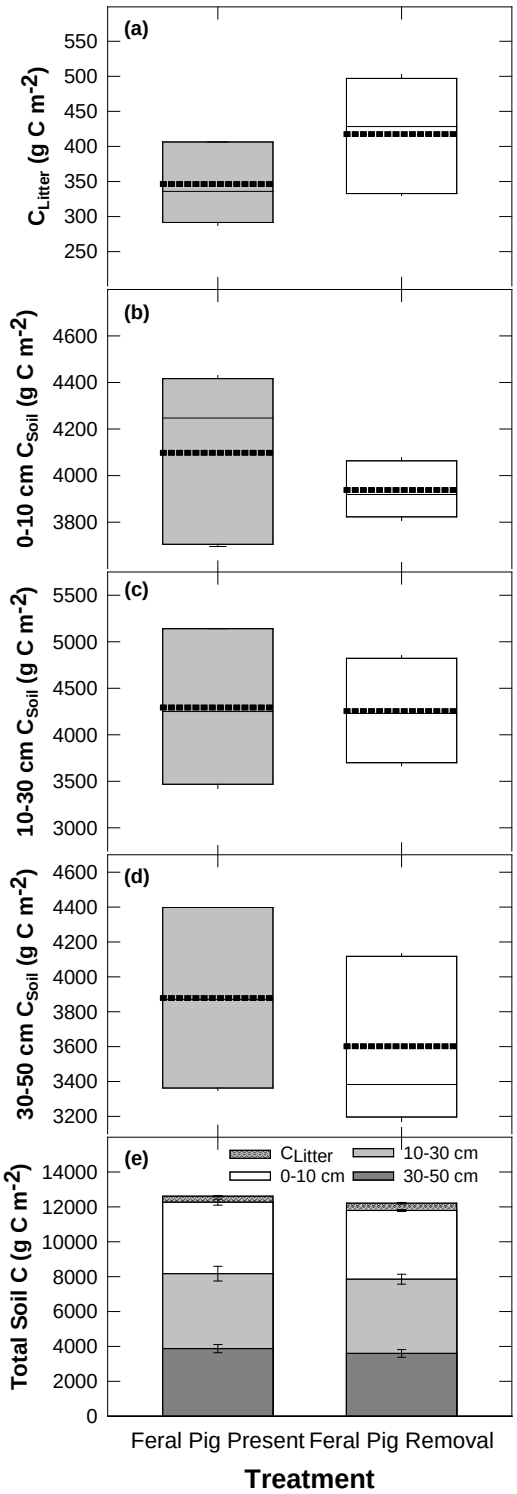

Figure 3.3 Feral pig removal did not impact (a) $C_{Litter,}$ (b) 0-10 cm C_{Soil}, (c) 10-30 cm C_{Soil}, or (d) 30-50 cm C_{Soil}. Box plot whiskers are absent due to small sample size; dotted lines indicate mean and solid lines indicate median values. (e) The vertical profile of soil C pools down to 50 cm did not change following feral pig removal. Error bars indicate SE for each soil C pool

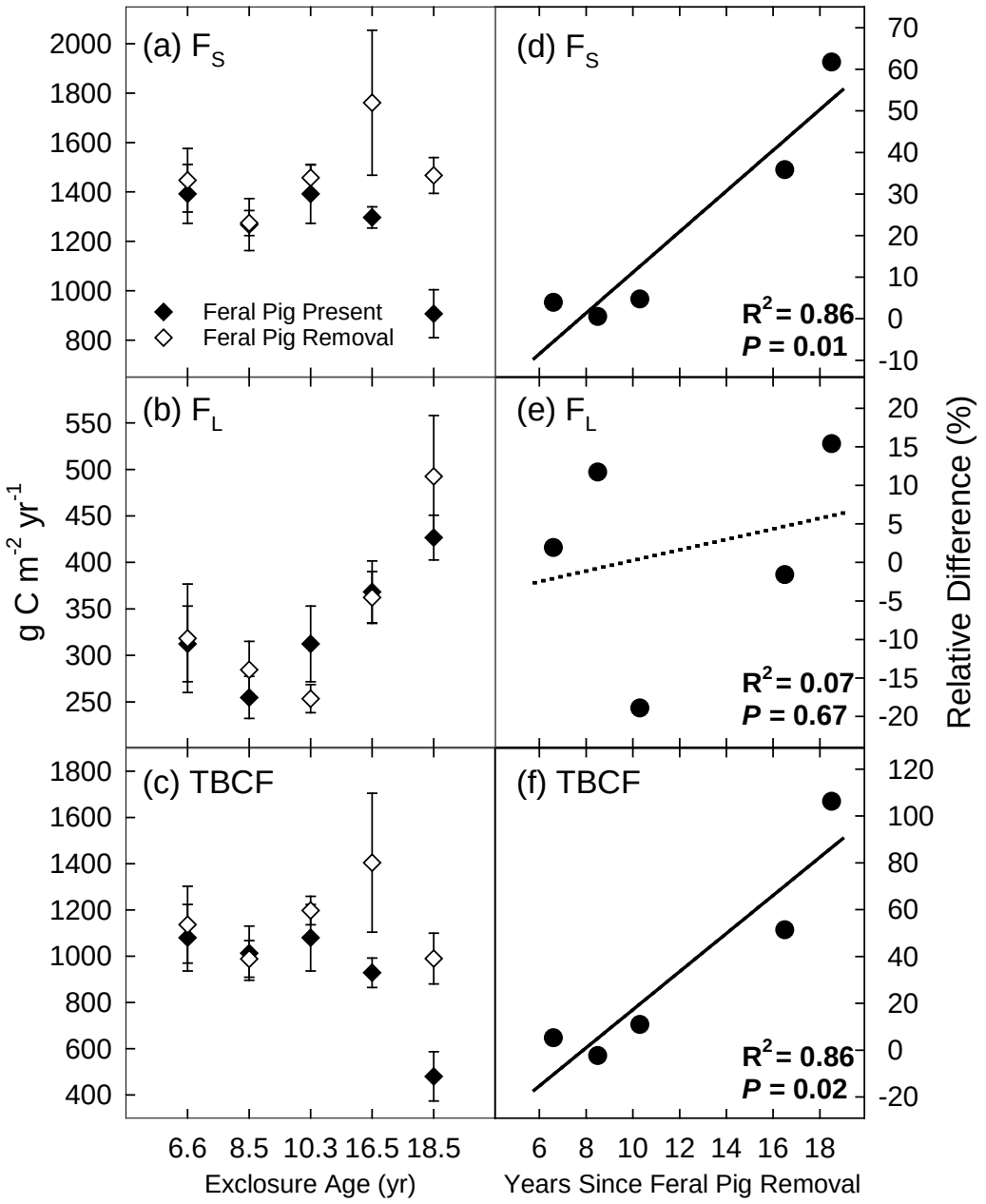

Figure 3.4 Mean annual (a) F_S, (b) F_L, and (c) TBCF (g C m^{-2} yr^{-1}) for paired sites across the chronosequence of five exclosures. Filled diamonds indicate values for feral pig present sites and open diamonds indicate values for feral pig removal sites. Error bars indicate SE. The relative difference (%) in (d) F_S and (f) TBCF had significant positive linear relationships with increasing time since feral pig removal ($\alpha = 0.10$). (e) F_L had no relationship with increasing time since feral pig removal. Relative difference is calculated as the % difference between means of paired sites: [(Feral Pig Removal – Feral Pig Present) / Feral Pig Present] * 100

Discussion

Nonnative ungulate removal has been shown to alter soil biological, physical and chemical properties (Chapter 2; Vtorov 1993; Kardol et al. 2014; Siemann et al. 2009), and to alter vegetation communities (Kardol et al. 2014; Siemann et al. 2009; Cole and Litton 2014; Hughes et al. 2014; Thaxton et al. 2010; Hata et al. 2014), which collectively can impact ecosystem processes given the tight linkage between aboveground and belowground (Metcalfe, Fisher, and Wardle 2011). Given the widespread distribution of nonnative ungulates globally, understanding the biogeochemical consequences of the increasingly common practice of ungulate removal for restoration is important to understanding impacts to soil C storage and terrestrial C cycling. Of particular importance is determining whether removal of nonnative ungulates impacts soil C pools and fluxes in concert with the recovery of soil properties and vegetation that is commonly observed following nonnative ungulate exclusion.

This study investigated the impact of feral pig removal from Hawaiian tropical montane wet forests on soil C pools and fluxes. Within the same chronosequence of feral pig exclosures used in this study, Cole and Litton (2014) found significant increases in vegetation and soil surface litter cover with feral pig removal. In addition, in Chapter 2, I documented that feral pig removal in this study system improves soil structure (decreased bulk density, increased soil aggregation, increased porosity) while enhancing soil nutrient availability (elevated nitrogen mineralization, labile C and plant available macronutrients). Collectively, these ecosystem responses to feral pig removal represent key mechanisms driving potential changes in soil C pools and fluxes.

In agreement with my first hypotheses, F_S increased with feral pig removal, and the relative difference between paired feral pig removal and feral pig present sites showed a strong, positive relationship with increasing time since feral pig removal. Understory vegetation cover and abundance increase significantly with feral pig removal (Cole and Litton 2014), so an increased autotrophic contribution to F_S from the recovering understory vegetation may explain part of the increase in F_S with feral pig removal. In addition, F_S likely responded to changes in soil physical, chemical and biological properties with feral pig removal (Chapter 2). In particular, Chapter 2 documents lower bulk density, lower volumetric water content, higher porosity, lower water-filled pore space, and more water stable aggregates with feral pig removal. These changes in soil properties likely elicited increases in autotrophic F_S via increased gas exchange and

diffusion, and heterotrophic F_S via greater soil microbial and faunal abundance and activity. These results are similar to Risch et. al. (2013) who found that exclusion of medium and large-sized ungulates (red deer [*Cervus elaphus* L.] and chamois [*Rupricapra rupricapra*]) stimulated an increase in F_S that was largely predicted by changes in soil properties (i.e., soil moisture and temperature). In contrast, Risch et. al. (2010) detected an increase in F_S following three years of wild boar grubbing, but this response could be an artifact of long term priming effects (Kuzyakov 2010; Zhang et al. 2017) following the incorporation of organic matter into the relatively nutrient-poor Swiss Alpine soils. In this current study in Hawaiian montane wet forest with high soil water content, soil faunal abundance and activity can be suppressed by compacted and saturated soils (Vtorov 1993; Wilkinson, Richards, and Humphreys 2009) that occur with feral pig activity (Chapter 2).

Across the chronosequence, F_L did not differ and showed no relationship with increasing time since feral pig removal, in contrast to the original hypothesis. This is likely due to F_L being dominated by overstory (i.e. *Metrosideros polymorpha*) and midstory (e.g. *Psychotria hawaiiensis* and *Cibotium glaucum*) constituents, whose total stem density and basal area did not vary with feral pig removal (Cole and Litton 2014). Although Cole and Litton (2014) found a significant increase in understory vegetation cover and ground-rooted woody plants <1 cm DBH following feral pig removal, the added contribution to F_L by the increase in newly established understory vegetation was overshadowed by extant canopy vegetation that constituted the majority of litterfall. F_L may also show a lagged response to feral pig removal, whereby the positive impacts of increased nutrient supply on vegetation growth sufficient for a detectable increase in F_L occurs over a timespan greater than that of the overall chronosequence (i.e., 18.5 years). Overall, the range of values for F_L across all sites (253.3 – 492.5 g m^{-2} yr^{-1}) aligns well with F_L from some of the most productive forests on Hawai‘i Island (Giardina et al. 2014), and highlights the magnitude of C input into the soil via F_L.

In support of my first hypothesis, there was an overall effect of pig removal on TBCF, with the relative difference between paired plots increasing with time since pig removal. Overall, the ranges of F_S (1274.3 – 1761.1 g c m^{-2} yr^{-1}) and TBCF (480.2 – 1374.9 g C m^{-2} yr^{-1}) measured across all sites align with values measured in similar forests by Litton et. al. (2011) and Giardina et. al. (2014), respectively, and highlight the rapid belowground soil C cycling of these highly productive Hawaiian tropical montane wet forests.

Importantly, and in agreement with my first hypothesis, accelerated belowground C cycling with feral pig removal did not impact C_{Soil} or C_{Litter}. Rather, soil C inputs are likely rapidly decomposed or stabilized in organo-mineral associations. These results are in line with a study on Hawai‘i Island which found that F_S (Litton et al. 2011), TBCF (Giardina et al. 2014) and litter decomposition (Bothwell et al. 2014) all increased with increasing mean annual temperature, while soil and ecosystem C storage were unaffected (Selmants et al. 2014).

Soil C saturation (Stewart et al. 2007) and/or soil mineralogy may also contribute to the lack of change in soil C storage with increased soil C cycling (Selmants et al. 2014). The primary weathering products of the young volcanic soils in this study system are characterized by amorphous, non-crystalline minerals (allophane, imogolite, and ferrihyrdrite) that form stable organic-mineral bonds and effectively protect and sequester soil organic matter for hundreds to thousands of years (Nanzyo 2002; Torn et al. 1997; Giardina et al. 2014). Consequently, C_{Soil} in these forests align with C_{Soil} measured in some of the most C dense forests in the world (Selmants et al. 2014). Given the tremendous amount of C stored in these soils, less than 20 years of feral pig removal may, therefore, not create substantial changes in clay mineral concentrations which impact long term soil C storage. However, improved soil structure with feral pig removal may support infiltration of dissolved organic C compounds to greater depths (Marin-Spiotta et al. 2011; Kramer et al. 2012), thereby facilitating increase C_{soil} at depths below those quantified in this study. Thus, the response of soil C storage to ungulate invasion and removal is likely determined substantially by soil physical, chemical and biological properties (Lehmann and Kleber 2015).

Conclusions

This study demonstrated that feral pig removal from montane wet forests on Hawai‘i Island increases the output of C from soils as soil-surface CO_2 efflux, which is often interpreted as a loss of soil C that would reduce storage capacity. However, increased soil CO_2 efflux was offset by a concomitant increase in C input to belowground via TBCF, and to a lesser extent F_L. Although belowground soil C cycling increased following feral pig removal, soil C storage did not vary, suggesting rapid decomposition of soil C inputs in response to improved soil structure and reduced water content following feral pig removal. Globally, removal and exclusion of feral pigs and other invasive ungulates from fenced management units is a common strategy for the

recovery of invaded ecosystems, and this study shows recovering vegetation and improved soil properties within protected ecosystems can alter soil C cycling, but changes in soil C storage will likely be dependent upon soil physical, chemical and biological properties.

CHAPTER 4

Conclusions

Nonnative feral pigs have invaded ecosystems on all continents except Antarctica, and most oceanic islands (Barrios-Garcia and Ballari 2012; Wehr, Hess, and Litton, *In press*). Feral pig foraging and wallowing are such significant disturbances to soil and vegetation (Spear and Chown 2009; Barrios-Garcia and Ballari 2012; Campbell and Long 2009), that feral pigs are considered the greatest non-human, animal-related extinction threat to native species (Gurevitch and Padilla 2004). Removal of feral pigs from fenced management units (i.e., exclosures) is increasingly common with well-documented positive impacts on vegetation recovery (Barrios-Garcia and Ballari 2012; Cole and Litton 2014; Cole et al. 2012; Siemann et al. 2009). Little is known, however, about the impacts of feral pig removal on belowground processes that influence vegetation recovery and soil carbon (C) dynamics. The research contained here, conducted across an 18.5 year chronosequence of feral pig exclosure in Hawaiian montane wet forest, demonstrates that feral pig removal improves soil properties, and increases belowground carbon (C) cycling with no significant impact to soil C storage.

My research documented that soil structure and nutrient availability increased across the chronosequence of feral pig exclosures. Specifically, feral pig removal increased extractable cations, labile C, soil aggregate stability, porosity, foliar $\delta^{15}N$, and resin available NH_4^+, while decreasing extractable P, bulk density, volumetric water content, water-filled pore space, resin available NO_3^-, and pH. Additionally, increasing time since feral pig removal was related to increasing nitrification. These results suggest that recovery of both native and nonnative vegetation following feral pig removal (Cole and Litton 2014) is at least partially the result of alterations to underlying soil properties. Changes in these soil characteristics potentially drive vegetation responses to the removal of nonnative ungulates elsewhere, but to date this has received little attention in the scientific literature.

Additionally, my research demonstrated that feral pig removal from tropical montane wet forests increases the output of C from soils as soil-surface CO_2 efflux, which is often interpreted as a loss of soil C that would reduce storage capacity and increase atmospheric CO_2. However, increased soil CO_2 efflux was offset by a concomitant increase in C input to belowground via total belowground C flux, and to a lesser extent annual litterfall. Although belowground soil C

cycling increased following feral pig removal, soil C storage remained unchanged, suggesting rapid decomposition of soil C inputs in response to improved soil structure and reduced water content following feral pig removal. Globally, removal and exclusion of feral pigs and other invasive ungulates from fenced management units is a common strategy for the recovery of invaded ecosystems, and this study demonstrates that recovering vegetation and improved soil properties within protected ecosystems can alter soil C cycling, but changes in soil C storage will likely be dependent upon soil physical, chemical and biological properties that can vary greatly across ecosystems.

Overall, this research addresses a knowledge gap in scientific understanding of the impacts of feral pig removal on soil biogeochemistry and provides land managers with additional information to support their restoration efforts. Furthermore, as more exclosures are constructed in the Hawaiian Islands and around the world, there is tremendous opportunity to expand upon this research and measure the response of soil biogeochemistry to nonnative ungulate removal globally. In particular, such changes in belowground ecosystem processes are important to understand in the context of rising atmospheric CO_2 levels and global climate change that can be accentuated or ameliorated by management of invasive species.

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